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PLEIOTROPIC GENE ACTION

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THE PHENOMENON OF PLEIOTROPISM

It has been found early in the history of genetics that the action of a particular gene may not be restricted to one organ. The albino gene, e.g., which is found in many mammals causes the formation of a white coat and of red eyes. Genes of this type which affect more than one organ system have been called *pleiotropic* by Plate (1910, 1913). Haecker (1925) proposed the term polyphaen for the same phenomenon; this term, however, has not come into general usage.

The developmental interpretation of pleiotropism is easy in the case of the albino gene. The facts in this case can be expressed by stating that the albino gene suppresses the formation of pigment wherever it occurs, i.e., both in the hairs and in the eyes. Most cases of pleiotropic gene effects are not so simple. The mutant gene *a* in the meal moth Ephestia, for example, reduces or suppresses the pigmentation in the adult eyes and testes, and in the larval hypodermis (Caspari, 1933), as well as in some other organs, but not in the pupal case and in the scales on wings and body (Kühn and Henke, 1930). Similarly, in Drosophila, many eye color mutants, such as *w, v, cn,* etc., affect at the same time the pigmentation of the Malpighian tubules, but not the color of the body (Brehme and Demerec, 1942). Some body color mutants, on the other hand, are known to affect the pigmentation of the larval mouth parts and the larval spiracle sheaths (Brehme, 1941). A similar case of pleiotropism affecting pigment patterns was already known to Mendel. He found that one of the genes he studied in the sweet pea influenced at the same time the pigment in the seed coat, in the flower and in the axils of the leaves. One of his strains had white seed coat, white flowers and lacked the axillary spot, while the other had a brown seed coat, colored flowers and possessed the axillary spot. These three characters always stayed together in breeding experiments, and were therefore regarded by Mendel as manifold effects of one factor (Mendel, 1866).

More or less complex patterns of pleiotropic gene action have been found in all organisms which have been examined genetically. In Drosophila, e.g., the mutant *vestigial* causes the formation of short wings, and influences at the same time the position of the bristles on the scutellum. *Rudimentary* affects the shape of the wings and of the hind legs, *cut* the

shape of the wings and of the arista, Ci^w (Cubitus interruptus Wallace) affects the venation of the wings as well as the formation of the legs. Effects on viability and fertility which are common pleiotropic effects will be discussed in a separate section.

A mutation producing a particularly complex pattern of effects has been described by H. Timoféeff-Ressowsky (1931) in *Drosophila funebris*. The mutant gene Polyphaen, a dominant, lethal in homozygous condition, causes at the same time rough eyes, abnormal abdomen, reduction of the bristles on head and thorax, incomplete wing venation and changes in the position of the wings. It is possible that the mutation *"Polyphaen"* represents a chromosome rearrangement. Another mutant with strongly pleiotropic effects in *Drosophila melanogaster, "polymorph,"* has been described by Neel (1942). In this case, eyes, wings, bristles, internal genitalia are affected. A number of other striking cases of pleiotropism in Drosophila are quoted in Neel's paper.

A large number of genes with pleiotropic effects have been observed in the mouse. Such a gene is the mutant "screw tail," described by MacDowell, Potter, Laanes, and Ward (1942). This mutant affects the development of the tail, vertebral column, sternum, jaws, and teeth. Furthermore the skull, the pelvis, the ears, and the eyes are affected. Reduction of growth and increased mortality may be at least in part caused by the deformation of the jaws and teeth which interfere with efficient feeding. In the tail the vertebrae appear normal at birth, but the tail is twisted due to shortening of the tendons. Later in development excentric reduction of vertebrae appears, leading to kinks in the tail. These reductions are interpreted as consequences of the tension and pressure exerted by the shortened tendons. In the lumbar and thoracic region, on the other hand, excentric vertebral reductions seem to be primary developmental disturbances, since many of the vertebrae appear already at birth with two centers of ossification per centrum whereas normal vertebrae have usually one. The vertebral centra appear frequently shortened. The pelvis appears normal, but it is displaced posteriorly with respect to the vertebral column, so that the 27th vertebra has the shape of a lumbar instead of being the first sacral vertebra, and the first caudal vertebra functions as a sacral.

The sternum, instead of consisting of 6 slender sternebrae, is one flat bone, broader and much shorter than the normal sternum. According to Bryson (1945), this deformity is a secondary effect induced by retardation of the growth of the ribs which are responsible for the normal shape and division of the sternum. This in turn is probably related to the shortening of the centra of the vertebrae. The lower jaw is shorter than normal. The roots of the molars are underdeveloped, and the grinding surfaces of the molars reduced. The roots of lower and upper incisors do not grow as far back in screw-tailed animals as in normals. At later stages of development, the resulting malocclusion of the incisors becomes stronger, and the forward growth of the incisors becomes inhibited, leading to increasingly severe abnormalities.

Many other genes with pleiotropic effects have been described in the mouse. Examples are the mutants "flexed tail," which induces kinky tail, embryonic anemia and spotting of the coat (Kamenoff, 1935; Grüneberg, 1942, a, c) and "short ears," affecting the skeleton as well as the pinna of the ear (Snell, 1931, Green and McNutt, 1941).

Many of the hereditary abnormalities encountered in man form syndromes of apparently unrelated effects which fit the definition of pleiotropism. As an example, phenylketonuric idiocy may be mentioned. In this condition, a mental defect is associated with a metabolic disturbance which leads to the excretion of phenylpyruvic acid in the urine. A third character of the syndrome is a reduction in

pigmentation of the hair; most phenylketonurics are light blondes.

The number of examples of pleiotropic genes could be multiplied indefinitely. Mutations with manifold effects are known from every organism which has been investigated genetically, plants as well as animals. Every mutant allele affects a certain number of characters while others remain unaffected. Hadorn (1945) described this finding by the term "pattern of manifestation" of a pleiotropic gene. This pattern of manifestation includes the particular organs in which effects of the mutant allele are observed, and the particular way in which the particular organ is affected. It should be pointed out that even in organs in which differences between mutant and wild type cannot be detected by morphological means, they may sometimes be found by more sensitive chemical or immunological methods. The application of more sensitive methods of observation will therefore tend to increase the area of manifestation of a particular allele. Hadorn has also pointed out that the pattern of manifestation can never reveal the complete activity of a particular locus, since it only shows the difference in action between two alleles, e.g., the mutant and the wild type. Beyond this "differential pattern" by which two alleles differ from each other there is still the "residual pattern" of gene action, those activities which are common to both mutant and wild type gene, and which cannot be observed.

It may be assumed that the total activity of a gene may be revealed by a study of small chromosome deficiencies involving not much more than one locus. But Hadorn concluded that not even small deficiencies can give a complete picture of the manifestation pattern of a particular gene since, in Drosophila at least, they are usually early lethals. Any potential activity of the gene occurring later in development would therefore not be detected by this method.

Developmental Analysis of Pleiotropic Characters

In many cases there is evidence that the different manifold effects of a particular gene are related with each other physiologically and developmentally. Evidence for this assumption is obtained, when in several independent mutations in the same species a similar pleiotropic pattern of manifestation is encountered. Brehme and Demerec (1942) found that the pigmentation of the Malpighian tubules may be affected by eye color mutants, but not by mutants affecting body color or other characters. A close relation between the pigment of the eye and of the Malpighian tubules seems therefore indicated.

In the mouse, Grüneberg (1948) has pointed out that in 13 out of 16 known mutations inducing waltzing behavior a triad of symptoms is found: waltzing, shaking movements of the head and deafness. Only in three mutants occur circus movements without shaking or deafness. Only one condition, probably due to multiple factors, has been found in which deafness occurs without any disturbances of the equilibrium (Caspari unpublished). It appears reasonable to assume that the disturbances of the equilibrium expressed in waltzing movements and head shaking, and the loss of hearing are physiologically related, particularly since the receptor organs involved in all these symptoms and some of the nervous mechanisms are closely related in place and development.

Dunn and Gluecksohn-Schoenheimer (1944, 1947) have described that in several different genotypes in both the mouse and the rat a syndrome consisting of reduction of the tail, imperforate anus, and abnormalities in the urogenital organs is encountered. Particularly in the mutant gene *Sd*, but also in other tail mutations and combinations of tail mutations, kidneys, urethra, and rectum may be reduced, missing, or histologically abnormal, in addition to the tail characters. It

is clear that a developmental relation between these characters must exist.

A developmental relationship between different pleiotropic effects of a gene may also be assumed if the pleiotropic pattern of manifestation can be reproduced as a phenocopy by environmental factors. The mutant gene *crc* (cryptocephalus), a pupal lethal in Drosophila, inhibits the evagination of the head and eye discs at pupation. At the same time, legs, wings and bristles are reduced in size, and the abdomen is enlarged and remains at an early state of development. The same pattern of effects could be reproduced by temperature shocks 9–10 hours after puparium formation (Gloor, 1945).

In a number of cases these developmental relationships have been experimentally established. In the mutant *a* in Ephestia it could be shown by transplantation experiments that wild type organs release a diffusible substance, necessary for the formation of the pigments of eye, testis and larval hypodermis. This substance is missing in *aa* animals. (Caspari, 1933). A similar situation prevails for the mutant *v* in Drosophila (Beadle and Ephrussi, 1936). In both cases the diffusible substance has turned out to be kynurenin, a metabolic product of tryptophane. The pigments of the eyes and Malpighian tubules in Drosophila, of the eyes, testes, and larval hypodermis in Ephestia are all derived from kynurenin, and are therefore concomitantly influenced by genes affecting kynurenin metabolism. The pigments of the body in Drosophila, of the scales and pupal case in Ephestia, on the other hand, are melanin pigments derived from tyrosin, and may therefore be influenced by different sets of loci affecting tyrosin metabolism.

Bonnevie (1934) and Plagens (1933) investigated independently the action of a mutation *my* in the mouse which causes a very variable syndrome, consisting of disturbances of the eye and of the feet. The eyes show frequently hemorrhages, microphthalmia, lack of a lens, cataract, open eyelids at birth, etc. In the extremities, clubfoot, syndactylism, polydactylism, and other abnormalities are encountered. Furthermore, a saddle-like inhibition of hair growth is often found in the back. The underlying condition responsible for all these effects is the presence of clear blebs of fluid under the epidermis in embryos 12 days old. These blebs migrate following the lines of least stress under the epidermis, and come finally to lie at the extremities, in the feet and in the orbit of the eye. In this final position they cause the formation of hematomas and thrombi and interfere with the normal differentiation of the organs. The origin of the fluid is not known with certainty. Bonnevie suggests that it is cerebrospinal liquor which in *my my* embryos escapes from the myelencephalon in larger than normal amounts, and therefore cannot be completely resorbed by the tissues. Plagens on the other hand considers the fluid as blood plasma, and believes that greater permeability of the capillaries is the underlying cause of bleb formation.

Another clear and striking case has been analysed by Grüneberg (1938) for a lethal condition in the rat. The primary effect in this case seems to be a generalized action on the cartilage appearing at birth. The histological abnormality can be observed in all cartilages if the animal survives sufficiently long, or if cartilage from lethal animals is transplanted into normal mice (Fell and Grüneberg, 1939). But it is particularly strong in the thoracic region where it leads to enlarged ribs and enlarged cartilages in the trachea. These morphological changes lead in turn to fixation of the thorax in inspiratory position and a narrowing of the lumen of the trachea. Both these conditions interfere with efficient respiration and result first in emphysema of the lungs and secondly over a variety of symptoms some of which are of a compensatory nature to death. The probable developmental relationships between these characters are indicated in Figure 1.

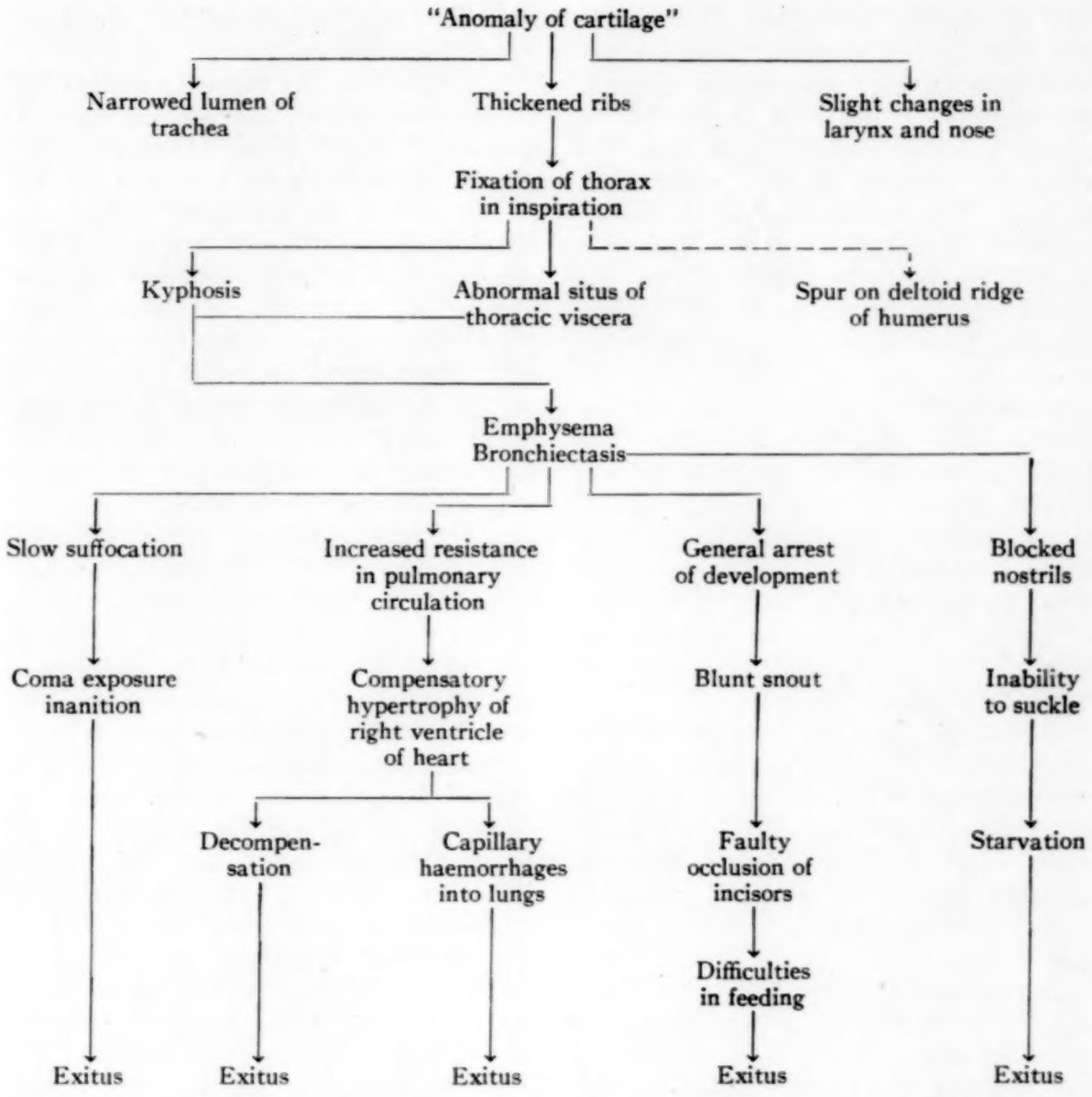

FIG. 1. Probable developmental relations of the pleiotropic effects in achondroplasia of the rat. From Grüneberg (1938).

Another condition in the mouse in which the developmental relations between the different phenotypic effects are well analysed is a mutant causing hydrocephalus (*ch*) (Grüneberg, 1943). Here, again, the primary effect is an abnormality of the cartilage which in this case first appears in embryos 12½ days old. At this stage, all cartilage appears abnormal histologically and retarded developmentally; but this histological defect is transitory, and in most cartilages the retardation does not lead to serious disturbances. Only the abnormal structure of the bones of the skull and of the nasal septum leads to enduring and finally fatal consequences. The basal cartilage of the skull is much shortened, and the fusion of the chordal and prechordal plate delayed. At the same time, the cerebral hemispheres grow strongly, just as in normal animals, and since the base of the skull is shortened are forced to bulge out dorsally. This bulging goes on against a considerable elastic resistance of the mesenchymal and skin tissues covering the head. These in turn press back on the posterior parts of the brain, particu-

larly the medulla oblongata. As a result, the parts of the medulla oblongata are telescoped together and appear stunted; the opening at the roof of the fourth ventricle through which fluid from the ventricles escapes to be absorbed is blocked. This obstruction leads to hydrocephalus, enlargement of the ventricles in the cerebral hemispheres. In the course of the formation of the hydrocephalus hemorrhages occur in the brain which finally lead to death. Other abnormalities found in *ch ch* animals are consequences of the hydrocephalus. The bones on the roof of the skull are not formed, since the bone-forming mesenchyme covering the cerebral hemispheres becomes thinned out. The stress exerted by the enlarged brain on the skin of the head is regarded as the cause for failure of the eyelids to close, and for abnormalities of the vibrissae.

A case in which the relations between the manifold effects of a gene are mostly compensatory is the mutant gene Frizzle in chickens (Landauer, 1942). The primary effect in this case is an abnormal keratinization of the feathers, leading in homozygous condition to complete loss of the feathers (Landauer and Dunn, 1930). Landauer and Upham (1935) have subsequently established a large array of manifold effects of this mutant, affecting the size and to a certain extent the histological structure of many internal organs. All these characters can be understood as compensations for the heat loss caused by the feather defect. The first consequence is an increased metabolic rate; the higher rate of metabolism necessitates in turn an enlarged heart, an increased volume of the circulating blood, and an accelerated rate of heart beat. Since the increased heat production calls for higher food uptake, the volume of the intestinal tract is increased in all its parts. The kidneys are also enlarged. The endocrine organs regulating the level of basal metabolism show definite changes. The adrenals are enlarged. The thyroids, depending on environmental conditions, may be either hypertrophied or show signs of exhaustion.

In Drosophila, the recessive mutant *lgl* (lethal giant larvae) has been extensively investigated by Hadorn. Larvae homozygous for this allele are unable to pupate. At the end of the last larval instar, the imaginal discs and germ cells appear degenerate, and the ring gland and salivary glands are retarded in development. Puparium formation is retarded or missing. The delay of puparium formation is due to the functional failure of the ring gland which controls puparium formation in the fly; implantation of normal ring glands leads to puparium formation in *lgl* larvae (Hadorn, 1937; Scharrer and Hadorn, 1938). The same appears to be true for the somatic parts of the *lgl* gonads which develop normally in a normal host. But not all of the pleiotropic effects of *lgl* are consequences of the failure of the ring gland; the germ cells of *lgl* testes and ovaries do not develop in a normal host, nor are normal testes injured by staying several days in an *lgl* larva (Hadorn and Gloor, 1942). In this case, therefore, the developmental connection between some, but not all of the manifold effects of the mutant is clarified. The same is true for the characters affected by the mutant grey-lethal in the mouse (Grüneberg, 1935, 1937). This mutant gene removes the yellow pigment from the hair. At the same time, all the bones of the body are abnormal and misshapen, and the teeth fail to erupt. The abnormalities of the bones can all be shown to be due to a single primary cause, failure of secondary absorption of the bones. The failure of the teeth to erupt, and the abnormal structure of the teeth seem to be due to the same cause. The resulting lack of erupted teeth hastens the death of the animals, but is not its only cause, since they die even on a liquid diet. No relation of the bone and teeth abnormalities to the effect of the same gene on coat color has been found.

All examples which have been de-

scribed so far are cases of "secondary" pleiotropism (Hadorn, 1945). That means that the manifold effects of a pleiotropic gene are subordinated consequences of a single primary action. This primary activity may affect every cell in the body. There is evidence that in all tissues of a^+ larvae kynurenin is formed, and that its formation is blocked in all cells in *aa* larvae. The phenotypic manifestation pattern, i.e., the distribution of pigment in the animal, is due to the fact that different types of cells acquire at different stages of development the ability of reacting on presence of kynurenin with pigment formation (Caspari, 1949). In this case, therefore, every cell seems to be primarily affected by the allele *a*. In other cases (achondroplasia in the rat, hydrocephalus in the mouse) it is a particular tissue which is affected at a particular time of development in a particular manner. In both achondroplasia and hydrocephalus the tissue primarily affected is cartilage. The difference between effects of the two mutant genes is primarily the time of activity and the histological picture of the abnormality. In both cases, all cartilages of the body seem to be affected, but in achondroplasia at least, to a different degree and at slightly different times. Grüneberg (1943) proposed that the primary effects of all genes are either cell specific or tissue specific. Organ specificity does not occur, and is always a secondary consequence of a general physiological or tissue change.

The reactions of the different tissues and organs on a primary general or tissue change are of different types. In some cases they are reactions to a chemical change, the chemical substance being necessary for a particular function (*a* in Ephestia, *lgl* in Drosophila). Related to this group would also be changes in an inductive stimulus. This has been suggested for the tail conditions in the mouse which at the same time produce abnormalities of the urogenital system and of the gut (Dunn and Gluecksohn-Schoenheimer, 1944). In hydrocephalus and in myelencephalic blebs in the mouse, on the other hand, many of the subordinated reactions seem to be mechanical consequences of the primary effect. Finally, there are secondary changes of a compensatory nature, as particularly well demonstrated in the Frizzle fowl.

Hadorn (1945) has considered the possibility that a single gene may have different primary activities in different types of cells. No evidence bearing on this point is available.

Grüneberg (1938) distinguishes between "spurious" and "genuine" pleiotropism. "Genuine" pleiotropism would involve several different primary activities of the same gene, while in cases of spurious pleiotropism there would be a single primary gene action which by means of one or more of the developmental mechanisms outlined in the preceding paragraphs would affect several organ systems. All cases considered in the present chapter are examples of spurious pleiotropism. It is Grüneberg's contention that genuine pleiotropism does not exist, and that cases in which a certain character cannot be fitted into the developmental picture, such as the pigmentation effect of the grey-lethal mutant, are due to our ignorance.

Grüneberg's postulate has in its favor its logical simplicity and its heuristic value. For it requires that in cases of pleiotropism developmental relations between the different characters should be looked for. Actually, a large number of embryological facts have been discovered by this method. This does not mean, however, that the possibility of genuine pleiotropism is excluded. As a matter of fact, even if present, it could not be demonstrated, due to our almost complete lack of knowledge about the primary action of genes. It is therefore of interest that genuine pleiotropism has actually been assumed for the *R*-series of alleles in maize (Stadler, 1946).

Four types of alleles are found in the *R*-series, all affecting anthocyanin pigments. R^r causes the presence of the

pigment in both aleurone and plant; in r^r anthrocyanin is present in the plant but absent in the aleurone layer; in R^g color is present in the aleurone but absent in the plant; while in r^g anthocyanin is missing in both structures. This situation could be easily understood as a case of spurious pleiotropism in which different alleles affect different cells differently, or act differently at different stages of development. Stadler's main argument is, however, drawn from the mutation behavior of these alleles. He found that in spontaneous mutation R^r mutates frequently into R^g and r^r but very rarely into r^g directly. The mutation $R^r \rightarrow r^g$ is, however, not so rare that it could be interpreted as a chance combination of independent mutations to R^g and r^r. It may be suggested from this finding that R is a "bipartite" gene. The two parts have similar effects, but in different tissues, cannot be divided by crossing over, but are able to mutate separately.

As will be shown in a later section, the behavior of pleiotropic characters in the process of mutation is highly pertinent to their interpretation. On the other hand, deductions from the behavior of multiple alleles are rather difficult, since, as will be shown in the next chapter, the expression of pleiotropic effects of multiple alleles does not necessarily follow any simple rules. Furthermore, mutation rates between different alleles of a series seem to be different in different cases. It seems to be preferable at the present time, to continue to analyze pleiotropic gene action on a developmental basis, but to keep in mind that genuine pleiotropism is not excluded.

Pleiotropic Characters in Series of Multiple Alleles

Multiple alleles are characterized by the fact that they do not show crossing-over, and that they usually affect the same character. If this character can be expressed in quantitative terms, the alleles will affect it to different degrees, and can therefore be arranged in a series of increasing effects.

If pleiotropic effects in such a series of multiple alleles are considered, it is found that sometimes they do not follow the same sequence. If they are closely related developmentally, they will vary concomitantly; but if their physiological relation is less close, they may show considerable independence. In Ephestia, a third allele to a^+ (black eyes) and a (red eyes) has been found, a^k (brown eyes). It is intermediate in eye color between a^+ and a, and the same applies to the pigmentation of testes and larval ocelli; the larval hypodermis is colorless, as in a. This may be interpreted to mean that the amount of kynurenin produced by a^k is intermediate between a^+ and a, and that therefore the pigments derived from kynurenin are intermediate in amount, the pigmentation effect being dependent on the threshold of the organ concerned. A number of cases of concomitant variation in series of multiple alleles has been given by Goldschmidt (1938).

At closer investigation, however, an increasing number of cases is found in which this relation does not hold. While in a^k in Ephestia all pigmentation characters are intermediate between a^+ and a, the speed of development is even lower than for a, so that for this character, the alleles would have to be arranged according to the series $a^+ > a > a^k$ (Piepho, 1934). In the alleles of the w-series in Drosophila, the pigmentation of the Malpighian tubules varies in most cases concomitantly with that of the eyes. But two alleles make an exception to this rule: w^{bl} is one of the darkest alleles as far as eye color is concerned, but the Malpighian tubules are very light. w^{sat} on the other hand, which has very light eyes, has bright yellow Malpighian tubules which cannot be distinguished with certainty from the wild type (Brehme and Demerec, 1942).

The W series in the mouse, consisting of three alleles +, W, and W^v, has two

pleiotropic effects: dominant spotting and macrocytic anemia. In *WW*, W^vW^v and WW^v, the fur is completely white with black eyes; the anemia is severe and lethal in *WW*, mild in W^vW^v, WW^v is intermediate with respect to anemia. The non-seriability of these effects appears in heterozygotes with wild type. *W*/+ heterozygotes are spotted, ranging from "all-whites" to full-colored animals, depending on genetic modifiers (Dunn, 1937). W^v/+ has not been studied so extensively; but the animals show spotting. A new character, however, appears in W^v/+ heterozygotes which is not found in *W*/+: a dilution of the coat color in the pigmented areas. In their anemia, the heterozygotes behave quite differently from the homozygotes. *W*/*W* animals have a severe lethal anemia, while *W*/+ heterozygotes are not anemic at all. With regard to red blood cell size a certain degree of heterosis is even found in *W*/+ individuals, the erythrocytes of the heterozygotes being even smaller than the wild type red cells (Attfield, 1951). W^vW^v mice have a macrocytic anemia much lighter than *WW*. In W^v/+ heterozygotes on the other hand, there is a definite though slight increase in the size of the red blood corpuscles as compared with normal, the blood corpuscles being intermediate in volume between W^vW^v and ++. It appears therefore impossible to arrange the three alleles in a series, when all characters in homozygotes and heterozygotes are considered (Grüneberg, 1942b).

Dominance and Penetrance of Pleiotropic Effects

It has been shown for the *W* series in the mouse that the dominance relations of different pleiotropic effects of the same allele do not behave in the same manner. For *W* the spotting effect is intermediate to dominant, while the anemia is recessive. A very striking case of this kind has been described for the mutant gene *Ri* in Oenothera (Weidner, 1950). *Ri* is a mutant in the *l* complex derived from *Oenothera odorata,* situated in an identifiable chromosome and linkage group. *Ri Ri* homozygotes are reduced in size. Their leaves are rolled into a tube, due to a higher growth rate of the lower side as compared with the upper side. There are a number of other pathological growth processes which lead to irregular proliferations and tumor-like conditions, particularly on the stem, on the hypanthia of the flowers and in the gynecea. These proliferations frequently show chloroplast-containing tissue and the amount of chlorophyll in *Ri Ri* plants seems generally increased while anthocyanin production is inhibited. Of particular interest is the fact that histologically the lower side of the leaf shows the palisade tissue usually characteristic of the upper side. The *Ri ri* heterozygote is intermediate between the two homozygotes in some characters: the rolling up of the leaves is present, but somewhat looser than in *Ri Ri* and appears somewhat later in development. The inversion of the histological structure of the leaves is much weaker than in *Ri Ri* plants, suggesting that it is not a direct consequence of the exposure of the underside by the rolling of the leaves. The proliferations, on the other hand, are usually absent in *Ri ri* heterozygotes. Finally, with regard to size, heterosis is usually found, *Ri ri* plants being even taller than *ri ri*. In the manifold effects of *Ri* all possible types of behavior are found in the heterozygote, ranging from almost complete dominance of *Ri* to recessivity and even heterosis.

Different pleiotropic effects react also differentially on dominance modifiers and on environmental conditions. H. A. Timoféeff-Ressovsky (1937) investigated the correlations in the degree of penetrance between different pleiotropic effects of the mutation *Polyphaen* in *Drosophila funebris*. She found that the penetrance values for abnormal abdomen and for abnormal wing venation showed a positive correlation. The expression

of two other characters, position of the wings and reduction of bristles, was not significantly correlated with these two effects nor with each other; rough eyes, a fifth effect of the mutant, showed 100% penetrance and consistent expressivity. For the variable characters it was found that their penetrance and expressivity varied in different degrees under the influence of temperature.

It has been mentioned earlier that the mutant *Sd* in the mouse causes a syndrome involving shortening of the tail and disturbances of the urogenital system which affect viability adversely. Dunn and Gluecksohn-Schoenheimer (1945) crossed the *Sd* strain out to two other strains containing modifiers for strong and for weak expression of the tail character. They found that in both cases the viability behaved inversely from the tail characters. This may be due to an action of genetic modifiers on the severity of the urogenital disturbances in the heterozygotes. The same strains contain therefore modifiers which increase the length of the tail in *Sd* heterozygotes and which increase the expression of the urogenital effects, and vice versa. In *Ki* in the mouse, the kinky tail has close to 100 per cent penetrance, in the heterozygote. But the occurrence of waltzing and deafness due to the same mutant gene is dependent on the presence of modifiers (Caspari, 1940).

All these findings agree in showing that multiple pleiotropic effects of one and the same gene may behave independently of each other, and quite differently, in heterozygotes and under the influence of modifiers. Grüneberg (1938) has suggested that in a series of subordinated pleiotropic effects the developmentally earlier ones will tend to show clear-cut dominance relationships while the more dependent ones will show more variability in their expression. This is also borne out in the Frizzle fowl, where the expression in the thyroid is most variable, varying from hypertrophy to complete exhaustion. Landauer considers therefore the thyroid as physiologically the weakest link in the compensatory changes occurring in the Frizzle fowl. It is doubtful, however, whether this principle can account for all cases of differential expression of pleiotropic characters.

Pleiotropic Effects in Generalized Characters

The mutant genes, whose effects have been reviewed in the preceding paragraphs, lead to severe abnormalities and frequently to death. They demonstrate the existence of pleiotropism, the developmental mechanisms by which it may be produced, and some general interrelations of pleiotropic effects. It has already been mentioned that mutant alleles with visible effects frequently influence such general physiological characters as viability, fertility, and speed of development. These pleiotropic effects seem to be of particular evolutionary significance. It has been suggested that most or all genes have pleiotropic effects of this type. The evidence bearing on this point will be reviewed in the following paragraphs.

In a classical study, Dobzhansky (1927) examined the effect of several well-known mutant genes in Drosophila on the shape of the spermatheca of the female. He found that certain strains carrying certain mutant genes had characteristic shapes of the spermatheca different from a wild type strain. After outcrossing to the wild strain, the F_2 segregated for spermatheca shape. In this segregation animals carrying the mutant characters showed a spermatheca shape different from wild type animals from the same cross. In the case of some mutants, *ebony, sooty* and *tan*^{2}, the different spermatheca shape of the mutant animals remained constant through up to 31 generations of outcrossing. In *cinnabar, yellow* and *white* strains the spermatheca shape tended to change toward the wild type shape in the first generations of outcrossing, but maintained finally a significant

difference from the normal animals. This indicates the presence of modifiers for spermatheca shape in these strains, but also the influence of the mutant gene itself. Of the mutant genes tested, only *star* and *singed* did not differ significantly from the wild type after outcrossing.

In heterozygotes, the spermatheca was frequently intermediate between both homozygotes. With respect to spermatheca shape, four alleles at the white locus would have to be arranged in the order: $w^i > w^+ > w^{e0} > w$. This does not agree with the seriation of the same alleles according to eye pigmentation, a situation which is frequently found in series of multiple alleles.

By selection, Dobzhansky succeeded in obtaining *yw* and w^i strains which had the same spermatheca shape as the wild type strain. If these animals were crossed to the original wild type strain the *yw* and w^i animals segregating in F_2 exhibited a spermatheca shape different from their wild type sibs. It is concluded from this experiment that the differences in spermatheca shape are actually characteristic of the mutant genes, and that in the selected strains their effects were masqued by the presence of independent modifiers.

These conclusions have been doubted by Schwab (1940). Schwab repeated Dobzhansky's experiment taking great care to insure isogenicity. Eleven recessive mutants were outcrossed for 20 generations to a specially prepared isogenic wild type strain. He compared the spermatheca shapes of the mutant and wild type sibs in succeeding generations of outcrossing and paid attention not only to the final values but also to the trends appearing during the course of outcrossing. His results are in good agreement with those of Dobzhansky. Two of the mutants had strong effects on spermatheca shape after 20 generations of outcrossing. In 5 the influence on spermatheca shape was small but still significant, in 2 it was doubtful, while only 2 mutants had no effect.

Schwab, however, does not accept that this result proves that the visible mutants in question were necessarily responsible for the differences in spermatheca shape, since even after 20 generations of outcrossing a sizeable segment of the chromosome linked to the visible mutant would not have been exchanged by crossing over. He concludes therefore that the effect on spermatheca shape may well be due to genes closely linked to the visible gene in question and ascribes it to the respective "chromosome segments."

Isogenicity except for one gene is an ideal state, and cannot be produced by any amount of outcrossing. Dobzhansky and Holz (1943) therefore used a different approach which settled the question. In a wild type stock, they induced visible mutations by means of X-rays, and compared animals homozygous for this induced mutation with the wild type strain. Nine out of 10 induced *yellow* mutations, all 4 induced *white* mutations, and 1 *vermilion* mutation showed definite effects on spermatheca shape. Two other mutants were ineffective. It should be emphasized that even the induction of mutations by radiation does not lead to real isogenicity, since with the doses of radiation employed other loci in the irradiated X-chromosome may be presumed to have mutated. If, however, two characters appear consistently associated in independent mutational events, their dependence on a single gene appears to be well established.

While therefore the pleiotropic effects of certain mutant genes in Drosophila on spermatheca shape are well established, the effects of certain color mutations on the body size of the mouse are still open to Schwab's objection. Certain color genes, such as *b* (brown), *d* (dilute) and A^y (yellow) seem to increase body size, while *se* (short ears), *ln* (leaden) and *pa* (pallid) appear to decrease it. Agouti and albinism have apparently no effect (e.g., Feldman, 1935; Castle, Gates, and

Reed, 1936; Castle, Gates, Reed, and Law, 1936; Castle, 1941). The argument in all cases is the difference in size and weight between animals carrying the mutant and its wild type allele in segregating crosses. The possibility that the size differences are due to genes linked to the respective color mutants can therefore not be excluded. Linkage between size and color genes has actually been assumed for *brown* by Green (1935). There is good evidence, however, that at least *se* and *d* really affect body size themselves. These two loci are closely linked. *d* increases body size, but *se* reduces it. In the double mutant *dse/dse* the body weight is slightly lower than in the wild type. If, however, one *se* is replaced by its normal allele, *d+/dse* animals are much heavier than the wild type. The presence of *se* in homozygous condition therefore decreases body size, even if *d* or a size gene linked to it is present (Castle, Gates, Reed, and Law, 1936). An influence on body size of the mutant *se* is therefore well established, and the same may appear likely for *d*.

Since the earliest times of genetics it has been observed that mutants frequently have a lower viability and fertility compared to their wild type sibs. Many mutant genes behave as semilethals, or influence viability and fertility adversely. These effects of visible mutants on viability were studied systematically by Timoféeff-Ressovsky (1934, 1935) in *Drosophila funebris* and *Drosophila melanogaster*. He crossed six different sex-linked mutants in *Drosophila funebris* for 20 successive generations to a highly inbred wild type strain. After this period of outcrossing, heterozygous females were backcrossed to mutant males, and the numbers of mutant and wild type animals hatching were counted. The results give values for the relative viability of homozygous mutant females as compared to heterozygous females and of mutant males as compared to normal males. Of the 6 mutant genes tested in this way, 5 decreased the viability significantly. The sixth, *ev* (eversae) showed in both sexes a viability slightly higher than that of the wild type. Combinations of two of these mutants exhibited a variety of possibilities, ranging from a greater reduction of viability to a viability higher than that of either mutant alone. Of particular interest is the fact that whereas *m* and *bb* reduce viability by 30% and 15%, respectively, the combination *m bb* has a viability as high as normal. Similarly, the presence of *ev* restores the viability of *sn* animals which without it have a viability of 79% (males) and 88% (females) of their normal sibs.

Similar results have been obtained by Kühn and Henke (1932) in Ephestia. For experiments of this type, Ephestia has the advantage of containing a large number (30 haploid) of small dot-shaped chromosomes of about equal size. If it is assumed that these chromosomes contain approximately equal amounts of genic material, over 96% of the whole gene complement must be assumed to be distributed at random in F_2, a degree of isogenicity reached only after many generations of outcrossing in Drosophila. Complete isogenicity, of course, is as hard to obtain in Ephestia as it is in Drosophila.

The data on the influence of visible mutations in Ephestia are derived as deviations from Mendelian expectations in F_2 and in the backcross to the recessive. The eye color mutant *a* has been shown in this way to decrease viability and to lengthen the time necessary for development. The recessive eye color mutant *t* restores the viability but not the speed of development of *aa* animals to normal, similar to the interaction of *ev* and *sn* in *Drosophila funebris*. Similarly, the wing color mutant *he* decreases viability and fertility and lengthens the time necessary for development (Kühn 1939). The adverse effect of *he* on viability is again compensated by the presence of the sex-linked wing color mutant *d*. *he he dd* develops still more slowly than moths containing *dd* or *he he* alone (Kühn and

Henke, 1935). An interaction of two independent genes in the opposite direction has been found in the moth *Ptychopoda seriata.* The eye color mutant *dec* does not affect viability, and the mutant *en* (dark larva) decreases viability only slightly. But in the double homozygote *en en dec dec* viability is strongly reduced as compared with the wild type (Kühn, 1941). The wing-color mutant *b* (black) in Ephestia decreases viability and increases the speed of development. In this case, the disadvantage in viability is found in F_2, but not in the backcross. This means that the heterozygote is equally viable with *bb,* and the homozygous wild type has a higher viability that either. In other words, *b* is recessive with respect to its effect on wing color, but dominant in its effect on viability. It should be recalled that this situation is not unusual in pleiotropic effects of one and the same allele.

The influence of some mutants and their combinations on the length of adult life in *Drosophila melanogaster,* and on their fertility has been studied by Gonzalez (1923). He finds a situation quite similar to that described for viability. Most mutants reduce adult length of life and fertility. Some, however, cause an increase in these characters. Combinations of two mutants each one of which decreases length of adult life may restore it to its normal value. Strohl and Köhler (1935), described a mutation *dia* in Ephestia affecting wing coloration which causes death of the adult moths in 1–2 days after eclosion, thereby decreasing fertility.

Of particular evolutionary importance is the effect of genes on viability under different environmental conditions. Timoféeff-Ressovsky (1934) investigated the viability of different mutants in *Drosophila funebris* under the influence of temperature and crowding. As mentioned above, *eversae* is somewhat more viable at 24–25 degrees centigrade than the wild type, but its viability is reduced below that of wild type at higher and at lower temperature. Females heterozygous for *Venae abnormes* are less viable than their normal sibs at high and medium temperatures, but at 15–16 degrees centigrade their viability is almost up to that of the wild type. *Bobbed,* on the other hand, is most reduced in its viability at low temperature, while at 28–30 degrees centigrade it approaches the viability of the normal. Every mutant has therefore its own temperature optimum.

Two factors constituting "viability" were examined separately, lethality at the egg and at the larval stages. It turned out that they are differentially influenced by the mutants and by temperature. The lowered viability of *eversae* at low and high temperatures is mainly due to increased larval mortality under these conditions while in *bobbed* the egg mortality is particularly increased at all temperature levels, but most conspicuously at low temperature. Crowding conditions also affect different mutants differently. Most mutants (*eversae, Venae abnormes,* for instance) show the highest survival in cultures with a small number of animals; but *bobbed* flourishes in overcrowded cultures.

The temperature dependence of viability effects of visible mutants may lead to a selective advantage over the wild type under certain conditions. This is exemplified by the semidominant melanistic mutation *At* (Atra) in *Ptychopoda* (Kühn and von Engelhard, 1937). In this mutant the speed of larval development at 18 degrees centigrade is much reduced and the pupae reach a larger size. The mutant is inferior to the wild type with respect to viability at high temperature (25° C.) particularly at low humidity. The mutant shows a significantly higher viability than the wild type at low temperature (18° C.) and high humidity. The mutant in this case has therefore a definite selective advantage over the wild type under certain environmental conditions.

In summation it can be stated that there is good evidence that many if not all

mutations influence such general physiological characters as size, viability, fertility, time of development, spermatheca shape, etc. These characters are known to be influenced by a large number of genes, and exhibit therefore the polygenic type of inheritance. It is important that some of these genes appear to be identical with well-known loci with definite phenotypic expression. The interaction of different mutant genes on viability shows that frequently a particular effect is not due to a particular gene but to a combination of genes. A disturbance of balance caused by one gene can be restored by the presence of another gene.

The question whether all these effects are actually due to the investigated mutant gene itself or to genes closely linked to it is definitely settled only for spermatheca shape in Drosophila. In the other cases it can only be stated that the evidence appears to support it and that, while doubt may remain in any single case, it is unlikely that in *all* cases linked modifiers are responsible for the effects on general physiological characters. Therefore the generalization that all genes affect such general physiological characters as viability, fertility, etc., can only be made in form of a hypothesis. It will be shown in the following chapter, however, that consideration of the chemical effects of genes lends strong *a priori* support to such a proposition.

Pleiotropic Effects at the Biochemical Level

If it is assumed that the primary gene action consists in a certain definite biochemical change, it should be concluded that secondarily other biochemical changes must result. Because of the close integration of biochemical processes in an organism, it is impossible to change one reaction and leave the remainder of the biochemical equilibrium unaffected.

This is borne out by the study of the mutant *a* in Ephestia. It has already been stated that in this mutant the conversion of tryptophane to kynurenin is inhibited. As a first consequence the pigments formed in wild type moths from kynurenin are suppressed. It could be shown furthermore (Caspari, 1946) that the amount of tryptophane is higher in *aa* than in wild type animals. In other words, the tryptophane which is not converted into kynurenin is stored in the organism. Further investigation demonstrated that the excess tryptophane is stored in the proteins, and that as a consequence qualitatively different proteins are formed in *aa* Ephestia. This was confirmed by the finding that wild type and *aa* proteins behave differently when attacked by autolytic enzymes (Casperi and Richards, 1949). In *v* Drosophila, tryptophane is also stored, but not in the proteins (Green, 1949).

It must be concluded from these experiments, that the chemical makeup of wild type and *aa* Ephestia cells must be different, quite aside from the presence and absence of pigment in the eyes and other organs. It may be suggested that one of these biochemical changes, possibly the qualitative change in protein composition, may be responsible for the reduction in viability and speed of development of *aa* animals.

The complex reactions caused by a biochemical block have been well demonstrated in Neurospora. Storage and excretion of an intermediate substance, its conversion into a pigment and its interaction with other chemical processes have been repeatedly found. The whole complexity of the system of interlocking synthetic processes has been well demonstrated by Emerson (1950). He discussed particularly the biosynthesis of the amino acids methionin and threonin and their interrelations. Examples of storage of intermediates, of inhibition by different substances, of alternate pathways in the synthesis of the same substance are found abundantly in this paper. One representative case will be described, following the interpretation of Emerson. The mutation in question is characterized by the facts that it grows

on minimal medium at 25° C., but needs sulfanilamide for growth at 35° C. It is inhibited by para-aminobenzoic acid, a substance which is known to be inhibited by sulfanilamide as an antimetabolite but also by the amino acid methionin. Threonin, on the other hand, permits growth of the strain even in the absence of sulfanilamide. Emerson suggests that in this strain a deleterious reaction takes place in which methionin or a related substance is used as a substrate, para-aminobenzoic acid as a catalyzer, and by which a requirement for threonin is produced. The reaction proceeds slowly at 25° C. so that the threonin need does not become critical, faster at 35° C. The deleterious reaction can be inhibited by sulfanilamide, since it inhibits the activity of para-aminobenzoic acid. Presence of the substrate methionin increases the rate of the deleterious reaction, particularly when the amount of para-aminobenzoic acid is not limiting. If a double mutant is produced which besides the mutant gene for sulfanilamide requirement contains another mutant inducing a requirement for methionin, this double mutant can grow in absence of sulfanilamide, if the methionin level in the medium is kept at a minimum. This situation recalls the restoration of viability of *aa* Ephestia by the gene *t*, and other examples of the same kind mentioned before. While the analogy is crude, and does not fit in all details, it gives a model how two different mutants may interact in restoring viability.

It appears that similar complex interactions of different substances—and of course the synthetic processes producing them—are frequent in Neurospora, though few of them are as clearly analyzed as the sulfanilamide requiring strain. The general conclusion that a mutation affecting a single metabolic step may indirectly affect a number of other reactions is therefore confirmed.

If complex metabolic reactions are changed in this way by the action of single mutant genes, it would be expected that the composition and structure of macromolecules such as proteins may be frequently affected by gene mutations. The case of the proteins of *a* Ephestia has been quoted above, and has been borne out by immunological techniques. Similarly antigenic differences have been demonstrated for the mutant *T* in the mouse (Caspari and Dalton, 1949) and for the mutant genes *v* and *rb* in Drosophila (Fox, 1949), and their wild type alleles. In the mouse and in Ephestia, an approach to isogenicity was attempted by repeated outcrossing, whereas the Drosophila mutants used by Fox were induced in a wild type strain by X-ray irradiation.

Conclusions

The last quoted examples indicate that the biochemical reactions occurring in the organism and consequently its biochemical constitution are pretty labile under the influence of genic and environmental changes. If mutations do not always lead to severe developmental abnormalities and a lethal result, this must mean that the normal developmental and biochemical processes are to a certain degree buffered against changes in a certain reaction. One possible mechanism of this buffering capacity may be suggested by the behavior of the sulfanilamide requiring Neurospora at 25° C. Among developmental mechanisms, the principle of double assurance, frequently encountered in embryology, may be mentioned.

In this way, a normal functioning of the biochemical and developmental mechanisms may therefore be present even under changed genetic conditions. Many variable characters, such as viability, fertility, spermatheca shape, do not appear to be so well protected against changes in the biochemical constitution of the cell. Changes in these characters are therefore frequently found accompanying gene mutations. This generalized picture of genic action makes it very unlikely that any mutation can occur which would not influence some characters of selective importance.

For normal conditions, the wild type is best adapted, and it is kept this way by selective pressure. The Ptychopoda strains used by Kühn and von Engelhard (1937) came from a Sicilian population, i.e., from a hot, relatively dry climate. The mutant *At* would be selected against under these conditions, even though it would be superior in a colder and wetter climate. The fact that melanistic mutants of Lepidoptera have become established in some regions in recent times may be due to changes in environmental conditions. The main conclusion that every mutant has its own environmental optimum, and that at this optimum it may under certain conditions have higher selective value than the wild type is well established and a fundamental fact for evolutionary processes.

To sum up, evidence exists that pleiotropic effects of genes are frequently found. The basis of this occurrence is the interaction of processes in the organism both at the developmental and at the biochemical level. General characters such as viability and fertility under different conditions are most generally affected by changes of genes, and it is these characters on which selective agents particularly act.

Summary

1. A large number of mutants is known which produce a syndrome of different effects in diverse organ systems. Developmental analysis shows that the mutant genes in question have a generalized effect on the organism or on a particular tissue which may or may not be restricted to a particular short period of development. Tissues which at this time are at a sensitive period will react most strongly. Due to the interrelation of different embryological processes, other tissues and organs may be secondarily affected. Compensatory changes in other organ systems are frequently found.

2. Pleiotropic characters in series of multiple alleles sometimes do not follow the sequence established from the expression of the most obvious character. Different pleiotropic effects of the same genes may exhibit different degrees of dominance or recessivity in the hererozygote, and are affected differently by genetic modifiers and environmental conditions.

3. General biological characters such as viability and fertility are frequently affected by genic changes. The pleiotropic nature of these effects on quantitative characters is well established for spermatheca shape in Drosophila, very likely for viability and duration of life in Drosophila and Ephestia, and for body size in the mouse.

4. Genic changes, even if they primarily influence one chemical reaction, secondarily would affect the whole biochemical equilibrium of the organism due to the interaction and coordination of chemical processes occurring in the cell. It is suggested that these biochemical changes are generally obtained as a result of gene mutations, and that the generalized biological effects are a consequence of the changed biochemical equilibrium.

5. The changes in general biological characters are acted upon by selection. It is shown that while the wild type is usually superior under ordinary conditions, mutants may be better adapted to different types of environments. Furthermore, the viability of mutants is strongly affected by other genes; several cases are given in which two independent mutants affect viability adversely, but the double mutant equals the wild type in viability.

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CHANGING THE GENE ORDER AND NUMBER IN NATURAL POPULATIONS

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INTRODUCTION

In *Drosophila melanogaster,* Ives (1950) discovered a number of suppressors of crossingover which he assumed to be chromosomal inversions. These supposed inversions were of exceptional interest since they had been produced due to the influence of a gene extracted from a natural population (the high mutation rate gene—*hi*). This gene increased the rate of gene mutations to ten times that observed in laboratory stocks and produced chromosome inversions at a low but measurable frequency. The author concluded that mutator genes are probably the major cause of spontaneous gene mutations and chromosomal rearrangements in natural populations. (The general significance of mutator genes has long been recognized. See particularly Demerec, 1937; Goldschmidt, 1939; and Neel, 1942.)

The probable significance of inversions in evolution was first clearly discussed and demonstrated by Sturtevant and Dobzhansky (1936) and Dobzhansky and Sturtevant (1938). The later work of both of these authors and of others (see Ives, 1947 and 1950, for other references) has both verified and extended the general hypothesis that in *Drosophila* inversions, which represent alternative gene arrangements upon which natural selection may act, are one of the major kinds of building blocks in the evolution of species.

Until the effects of *hi* became known, almost the only instances of *de novo* chromosome aberrations available for study were ones produced by irradiation of a type not believed to be an important part of the natural environment. Thus it is of particular interest to study a series of inversions which arose due to natural causes, since they should be more nearly the kind which have a chance to contribute to the intra-karyotypical diversity of the natural population. The present report is concerned with the findings resulting from a cytogenetic analysis of these chromosomal rearrangements.

MATERIAL AND METHODS

The material to be analysed consisted of 13 X-chromosome mutant stocks which originated in the experiments of Ives (1950). By means of crossover tests, each of these stocks had been shown presumptively to carry an inversion. (In one case, the exact source of the inversion within the experiments is not known and it will be dealt with only cursorily.)

These chromosome aberrations arose with a frequency much too large to be considered as not due to the effects of *hi*. The frequency amounted to 4.8% of the tested lethal-bearing chromosomes.

The chromosomal aberrations were maintained as stocks by balancing them with another X-chromosome inversion (*delta-49*). For cytological tests, each stock was then crossed to a strain with normal chromosomes, and salivary gland smear preparations were made from the resulting larvae, using the standard aceto-orcein procedure. The slides were examined and those showing the *delta-49* inversion were discarded. The remaining slides were analysed and the points of chromosome breakage in each aberration were described in terms of the standard salivary gland chromosome map of Bridges (1938). When two stocks appeared to have one break in common,

each was reanalyzed to determine more exactly the locus of the breaks. Therefore, a break which is the only one in that region of the chromosome found in this sample is not as accurately located as are those breaks which were similar in two or more stocks. No attempt was made to describe in detail those breaks occurring in the cytologically difficult heterochromatic region 20.

Description of the Aberrations

All of the stocks analysed proved to contain an aberration in the X-chromosome. Each of them is described below in terms suggested by Bridges and Brehme (1944). The general symbol, *In(1)hi,* indicates that the stock carries an inversion in the X-chromosome (chromosome number one) and was derived from experiments with *hi.* None produced any phenotypic effects in heterozygous females. Symbols such as 12E, 1F, and 4D refer to particular regions of the salivary gland chromosome. Hemizygote is the term used for the condition of the unpaired sex-linked genes in males.

In(1)hi 1. Breaks at 12E and 20. A recessive phenotype, droop wings, is associated with the inversion, probably as a position effect. Hemizygous and homozygous individuals are highly viable and fertile.

In(1)hi 2. Breaks at 1F and 20. Lethal when hemizygous.

In(1)hi 3. Breaks at 4D and 20. Lethal when hemizygous.

In(1)hi 4. Breaks at 4C and 20. Hemizygous individuals rarely survive, have rough eye, are sterile.

In(1)hi 5. Breaks at 1F and 20. Hemizygous individuals rarely survive, develop slowly, are small and sterile.

In(1)hi 6. Breaks at 4C and 20. Lethal when hemizygous.

In(1)hi 7. Breaks at 12E and 20. Lethal when hemizygous.

In(1)hi 8. Breaks at 3C and 20. Hemizygous individuals rarely survive, have rough eye, are sterile.

In(1)hi 9. Breaks at 8F and 20. Lethal when hemizygous.

In(1)hi 10. Breaks at 4E2,3 and 8A1,2. Hemizygous individuals rarely survive, have bulge eye and multiple effects, are sterile.

Tp(1)hi 11. A transposition, with breaks at 5C, 7E, and 20. The region between 5C and 7E is inserted into region 20. Lethal when hemizygous.

In(1)hi 12. Breaks at 1C3 and 20. Lethal when hemizygous.

In(1)hi 13. Breaks at 4E and 20. Lethal when hemizygous.

Distribution of Breaks on the Salivary Chromosome

Figure 1 shows the extent of each inversion in terms of the 20 major regions of the salivary gland X-chromosome map. In this figure the line across the top represents schematically the normal map of these regions, each of which is numbered and some of which are also subdivided by letters. Parallel to and beneath this map are lines representing the 13 inversions. In each case only the part of the chromosome involved in the inversion is represented. A long line represents a long inversion; a short line, a short one. In terms of the kinetochore, which is the spindle fiber attachment point and is located at the right end of the map, the left end of each line is the locus of the distal break and the right end is the locus of the proximal break, which breaks, occurring together, made possible the inversion. By following each of the 20 regions vertically from top to bottom through these 13 cases, it is possible at a glance to see how their breaks are distributed in the 20 regions.

It is obvious at once that the distribution of the breaks in this sample of inversion is not random among the 20 regions of the salivary gland chromosome map. Most striking is the fact that all but one case show one break in region 20. All of the other breaks occur in only 5 of the 19 remaining sections. In four cases,

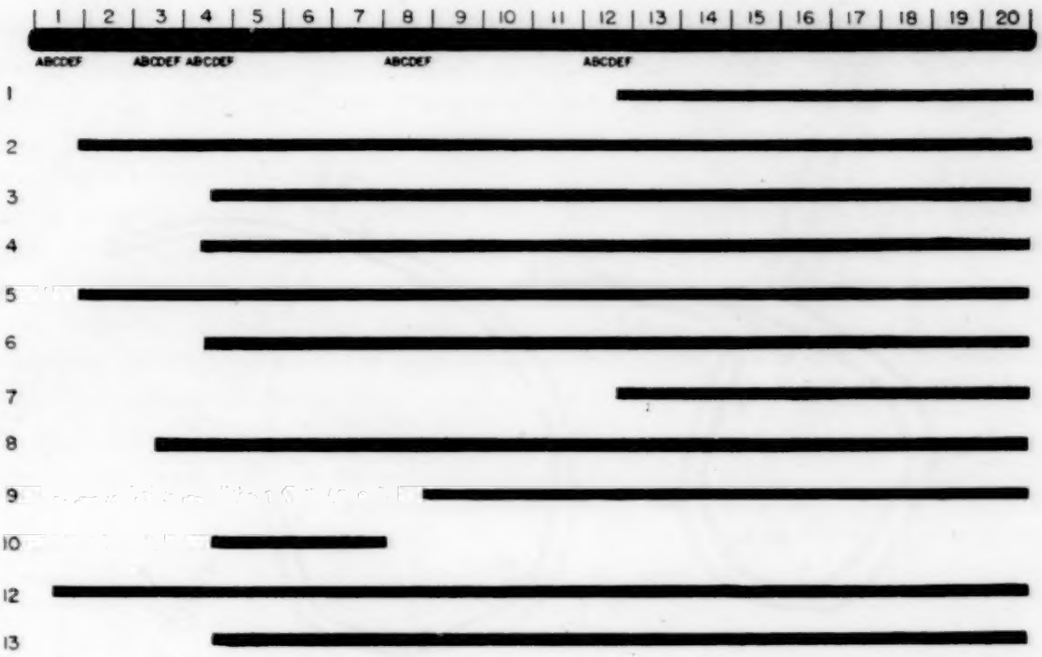

FIG. 1. The extent of the various inverted regions is plotted in terms of the major regions of the salivary gland X-chromosome (top). The code number of each inversion appears at the left.

two breaks occur at an apparently identical locus. Almost half of the left-most breaks occur in region 4. It appears from this that the high mutation rate gene which induced these chromosome breaks affects some regions much more readily than others. Nearly all of these regions coincide with ones found by Kaufmann (1939) to break with a high frequency when subjected to X-radiation.

EVIDENCE FOR SEVERAL LOCATIONS OF BREAKAGE IN REGION 20

Region 20 of the salivary gland chromosome is principally a heterochromatic region, that is, a region consisting largely of non-genic material with different biochemical properties than the other 19 regions as a group. It is diffuse in appearance and does not lend itself to an exact cytological analysis of inversion breaks that occur within it. Furthermore, even though it represents only one-twentieth of the salivary gland chromosome, it represents about one-third of the chromosome in the dividing cells in the same organism (Kaufmann, 1934). Accordingly, breaks found in region 20 actually could be widely separated on the chromosomes in which the initial breaks occurred. It seemed important to identify the breaks in region 20 more exactly for two reasons: first, to see whether there is only one section of this region affected by the high mutation rate gene; and second, to see whether two inversions which have apparently identical distal breaks are really identical inversions.

It seemed likely that the amount of crossingover manifested by the various regions of the chromosome would depend in part upon the location of the proximal break in region 20. It would differ in cases where the break occurred at the beginning of that region as compared with those in which the break occurred near the end of the region. Two such inversions are shown schematically in figure 2. The pairing chromosomes represent a normal chromosome (with gene symbols) and an inversion one (with numbers) whose proximal break in region 20 (stippled) is, in one case, near the kinetochore and, in the other, near the distal end of region 20. The distal breaks of these two inversions are represented as being at the

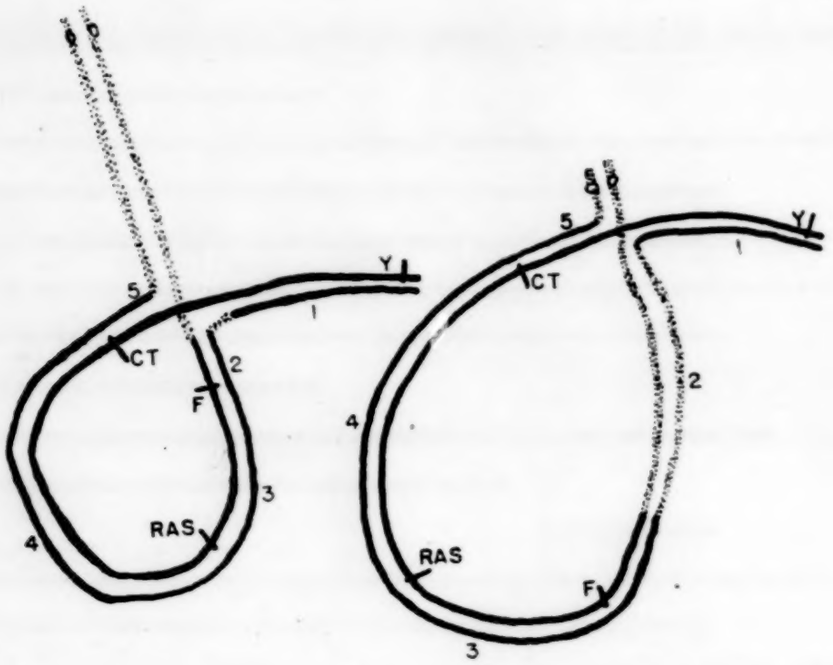

FIG. 2. Two types of inversion loops depending upon the position of the break in region 20 (the stippled part). The possible crossover regions are numbered: 1, between *y* and the distal break. 2, between the distal break and *f*. 3, between *f* and *ras*. 4, between *ras* and *ct*. 5, between *ct* and the proximal break. In the leftmost figure, region 2 is relatively short as compared to its length in the rightmost figure. The location of *ct* changes in the two figures in relation to the kinetochore (proximal to region 20).

same locus between numbers 1 and 2 on the inversion chromosomes. It can be seen that the amount of region 20 transferred to lie between numbers 1 and 2 is different in the two inversions, as is also the distance from the kinetochore to genic material (the solid line). In salivary-gland preparations these two inversions would give figures not recognizably different from each other. But the amount of crossingover detected by standard genetic tests should be noticeably different because of the actual differences which are figured here.

Because of the method used for detecting them, all but one of these inversions have hemizygous lethal effects which kill all or nearly all males carrying that part of the chromosome. Therefore, only the reciprocal classes of the lethal-bearing chromosomes are expected to appear in males. In each case, the inversion chromosome was matched heterozygously against a chromosome carrying four recessive mutant genes (*yellow* body color —*y*, *cut* wing—*ct*, *raspberry* eye color—*ras*, and *forked* bristles—*f*). The heterozygote was then backcrossed to males carrying the recessive genes and the offspring were classed according to the various possible phenotypes resulting from crossingover. A summary of the crossover data is presented in table 1. Presented in table 2 is a summary of the amount of crossingover in the various inversion X-chromosomes, region by region, using the mutant genes and the breaks of the inversions as the limits of the regions. The solid line at the top represents the normal chromosome, the dotted line at the end of it represents region 20. The numbers on the line are the amount of crossingover (in percentile units), which is normally observed in the sections between the marker genes used in these tests. Beneath this line and parallel to it are interrupted lines which represent the inversion chromosomes which were tested for crossingover. The simple gaps in these lines represent the normal alleles of the

marker genes. The breaks are represented by vertical bars. The number of sections of solid line in each case represents the number of regions in which detectable crossingover is possible, and the numerical value on each section of solid line is the amount of crosingover observed in these tests. The cases have been grouped so as to have adjacent to each other in this figure those inversions which were most similar in the cytological analysis.

As indicated in table 2, chromosomes 4 and 6 appeared cytologically to be very similar, but in terms of crossingover they are very different. Chromosome 4 averaged more than twice as much crossingover as chromosome 6. Exactly similar is the case of chromosomes 2 and 5—cytologically, indistinguishable; in terms of the amount of crossingover occurring in these tests, quite different. The most logical assumption for explaining this difference

TABLE 1. *The number of individuals in each phenotypic class resulting from crossingover between an inversion chromosome and a chromosome carrying the genes* y ct ras f

‡	*y ct ras f*	+	*y*	*ct ras f*	*y ct*	*ras f*	*y ct ras*	*f*	*y ras f*	*ct*	*y f*	*ct ras*	*y ct f*	*ras*	*y ras*	*ct f*
1	131	(117)	(50)	40	(12)	18	(3)	3	0	0	0	0	0	0	0	0
	93	82	25	28	7	12	1	1	0	0	0	0	0	0	0	0
2	247	0	14	0	4	0	16	0	8	0	27	0	5	0	1	0
	229	254	13	10	13	7	6	10	3	1	28	27	3	7	0	0
3	439	0	3	0	7	0	8	0	0	0	0	0	5	0	0	0
	400	442	7	5	10	10	5	8	0	0	0	1	7	9	0	0
4	911	18*	4	9	14	0	13	0	0	0	0	0	6	0	0	0
	671	485	8	8	5	9	5	16	1	0	2	4	4	4	1	0
5	329	7†	8	0	7	0	3	0	1	0	19	0	4	2†	0	0
	298	303	10	15	5	0	3	3	2	1	17	12	6	10	0	0
6	287	0	0	0	2	0	1	0	0	0	3	0	1	0	0	0
	265	268	0	0	0	0	0	1	0	0	1	1	1	3	0	0
7	120	0	0	69	0	17	0	5	0	0	0	0	0	0	0	0
	116	141	47	67	17	14	1	2	1	2	1	0	0	0	0	0
8	365	14*	7	0	10	0	16	0	1	0	5	0	6	0	0	0
	136	148	0	2	0	6	3	5	0	0	2	2	4	2	0	0
9	145	4	0	17	0	4	1	0	0	0	0	0	0	0	0	0
	125	240	22	17	2	1	1	0	0	0	0	0	0	0	0	0
10	295	13**	0	1	11	0	112	1**	0	0	0	1	0	0	0	0
	227	300	1	0	11	9	55	54	0	0	0	2	0	1	0	0
11	552	0	1	3	0	0	3	0	22	0	0	0	0	0	24	0
	395	459	9	2	0	1	5	6	85	0	0	0	0	1	68	0
12	139	0	9	0	5	0	4	0	2	0	15	0	6	0	0	0
	23	32	0	1	0	0	1	1	0	0	4	0	0	0	0	0

* Rough eye, rst type.
† Small, late hatch.
‡ Number of stock.
** Pleiotropic, bulge eye predominant.
( ) Droop wings.

TABLE 2. *The percentage of crossingover, region by region in the various inversions. The vertical bars in each case indicate a break of the inversion. The cases are grouped according to the position of the break*

STOCK NO.	Y	20	CT	12.8	RAS	23.9	F	9.3	
3		1.1	0.7	3.5		3.7		3.5	?
8		1.2	1.3	3.9		6.1		5.5	?
4		1.4	0.4	2.0		2.5		2.8	?
6		0.0	0.8	0.8		1.4		0.5	?
1		22.9		9.2		1.3	0.0	0.0	?
7		30.2		8.2		1.5	0.0	0.0	?
2	0.0	14.2		5.6		13.9		10.1	?
5	0.0	8.0		3.6		7.3		4.9	?
12	0.0	12.8		5.7		13.5		9.0	?
9		9.7		1.2	0.0	0.3		0.3	?
10		0.5	0.0	0.0	2.9	20.7			

seems to be that the proximal breaks of chromosomes 2 and 4 are as different from those of chromosomes 5 and 6 as are the proximal breaks figured in the inversion chromosomes of figure 2. Only in chromosomes 1 and 7 do both the cytological and the crossover data suggest an exactly similar pair of inversions, and in this case the differences in phenotype and viability of the hemizygote at once differentiate the two inversions. Thus it is reasonable to conclude that no two of these inversions represent completely identical cytological events, in spite of the fact that the chromosome breaks leading to the inversions are not distributed at random among the 20 regions of the map.

THE TRANSPOSITION

The case of the transposition of a small section of the chromosome to a new region, following three breaks in the chromosome, warrants special consideration. Attention was first directed to this case by the fact that crossover tests (table 1) gave results inconsistent with the tests on the other stocks, and not in line with expectation if the case were only a simple inversion. Not only were reciprocal classes unbalanced, but genetical triple-crossovers exceeded double-crossovers and each of these far exceeded single-crossovers.

When the cytological picture (fig. 3) was correlated with the crossover data, an unexpected and simple solution resulted. Due to the nature of the pairing necessitated by this chromosomal aberration (fig. 3) a crossover in certain regions will

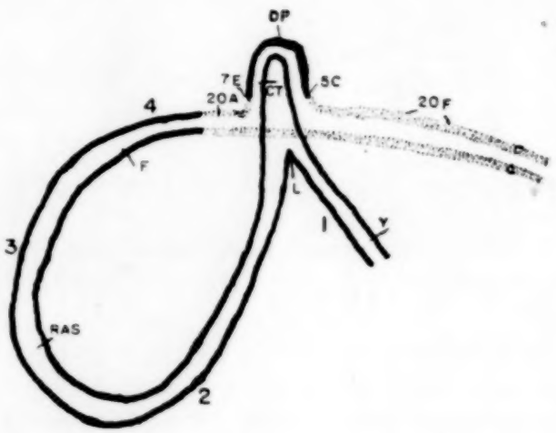

FIG. 3. The method of pairing of Tp(1)*hi* 11 with the *y ct ras f* chromosome. The numbers indicate the region of the salivary gland chromosome; the numbers in parentheses, the crossover region.

result in a new chromosome which carries the full complement of genes in normal order and, in addition, a duplication of regions 5C to 7E of the salivary chromosome —over one-tenth of the length of the salivary chromosome. This chromosome may be represented in simple form as:

$$\text{regions } \frac{1\,2\,3\,4\,5\,6\,7\,8\,9\,10\,11\,12\,13\,14\,15\,16\,17\,18\,19\,\;20}{} \text{---} \frac{5\,6\,7\;\;20}{\text{Dp}} \text{---0--}.$$

This new chromosome, containing the duplication, is viable both hemizygously and heterozygously; but the reciprocal crossover chromosome

$$\frac{(1\,2\,3\,4\,\;\;8\,9\,10\,11\,12\,13\,14\,15\,16\,17\,18\,19\;\;\;\;20\;\;\;\;)}{\text{l}} \text{------0--},$$

carrying a deficiency for these regions, is lethal (l) in each of those conditions. The viable crossover chromosome carries in its duplicated section the cytological region in which *ct* is located, with a normal allele at that locus. The presence of this one normal allele is sufficient to make a normal wing when *ct* itself is present at the other chromosomal position either hemizygously or homozygously. Since the new chromosome does not express the lethal hemizygous effect of the original *Tp* chromosome, that effect must therefore have been located at the place from which the piece of chromosome was transposed, and not at one of the places where 5C to 7E healed into region 20. From this, it can be seen that the observed discrepancies in crossover classes were actually due to single crossovers in which the effects of both the lethal factor and of the *ct* allele had been overcome as a result of the new chromosome thus formed. The extra genes present in the duplication following such crossingover apparently disturb the genic balance so as to cause the males, which are diploid for roughly one-tenth of their sex-linked genes, to be sterile as well as less viable than normal males. Triploid in the females, these same genes show no appreciable deleterious effects.

On the basis of the assumptions present in the above analysis it is possible to predict the expected phenotypes resulting from crossingover between the *Tp* and *y*

TABLE 3. *The predicted genotypes resulting from crossingover between Tp* (*1*)hi *11 and* y ct ras f, *and the actual flies classified according to phenotype*

A crossover in regions	Resulting genotype	No. males	No. females	% of total	Reciprocal genotype	No. males	No. females	% of total
(1)	*y l* Dp.		*		*ct ras f*	3 *	2 *	0.31
		1	9	0.62				
(2)	*y ct* Dp.	*	*		*l ras f*	0	0	0
(3)	*y ct ras* Dp.	24 *	68 *	5.62	*l f*	0	0	0
(4)	*y ct ras f* Dp.	22 *	85 *	6.54	*l*	0	0	0
(1) and (2)	*y l ras f*	0	0	0	*ct* Dp.	0 *	0 *	0
(1) and (3)	*y l f*	0	0	0	*ct ras* Dp.	0 *	1 *	0.06
(1) and (4)	*y l*	0	01	0	*ct ras f* Dp.	0 *	1 *	0.06
(2) and (3)	*y ct f*	0 *	0 *	0	*l ras* Dp.	0	0 *	0
(2) and (4)	*y ct*	0 *	0 *	0	*l ras f* Dp.	0	0 *	0
(3) and (4)	*y ct ras*	3 *	5 *	0.49	*l f* Dp.	0	6 *	0.37

Total flies counted, 1,636.
For the position of the crossover regions refer to figure 3.
* indicates the class is predicted to be viable. All other classes are expected to be inviable.
Dp. means the region carrying the wild type allele of *ct*.
l means the lethal effect associated with the deficiency created by the removal of Dp. to region 20.

ct ras f. The predicted viable classes of offspring are indicated in table 3 by an asterisk. In the same column of the table are the actual results of the crossover test. The correspondence between expectation and observation is statistically good when allowance is made, first, for the fact that the total number of individuals is sufficiently small so that in some instances no representatives of a class were obtained, and, second, that the males carrying the duplication have reduced viability.

Discussion

The importance of mutator genes in supplying natural populations with the variability needed for evolution of the population was suggested by Ives (1950). The present report shows that several types of chromosomal rearrangements contribute to the variability set up by mutator genes.

The non-random occurrence of the breaks involved in the chromosomal rearrangements is worth further consideration. Because of this it is possible for certain types of rearrangements to reoccur with a much higher frequency than would be possible if breaks were at random. This means that if one of these arrangements of genes should prove to be beneficial, the population would have a ready supply of the particular arrangement, and evolution could proceed more rapidly than otherwise.

There are two facts about these inversions which suggest that mutators may act primarily through heterochromatin in producing chromosome breakage. First, in all but one case, one break was in region 20, which is definitely heterochromatin. Secondly, all of the other breaks encountered in this group of inversions occurred in one or another of the few regions in the X-chromosome which Kaufmann (1939) suggests contain interstitial heterochromatin.

If it is true that mutators produce inversions through their effects on heterochromatin, then the location of inversions (and thereby the particular gene sequence) produced would depend upon the position of heterochromatin on the chromosome in a particular population. Thus a population would not be limited in the long run as to the particular inversions it could acquire, but only at any one time, assuming that the heterochromatin can change position. The work of McClintock (1950) certainly shows that this is possible. In fact, the very occurrence of one inversion involving a break in heterochromatin alters the position of some of the heterochromatin and offers a field within which the mutator gene can cause a different end result.

A transposition is a means by which first an individual, then by gene drift and selection, a population, and finally a species, can increase both the number and kind of genes in its genotype or pool. The number of genes, as is shown in this study, can be increased by crossingover after the transposition has taken place. The kind of genes can be expected to increase by mutations of old genes to new biochemical entities in the loci which exist in duplicated condition following the crossingover. In the present instance the transposition was caused by a naturally occurring agent, a mutator gene. This, then, is a mechanism by which evolution can proceed more rapidly in a natural population with such mutators in its gene pool, since such a population would thus be provided with a wider range of potentially adaptive genetic variability than would otherwise be possible.

The acquisition of duplicated gene loci could be the principal initial step by which a species receives new genetic material and ultimately new variability due to position effect, recombination, and mutation. Goldschmidt (1950) objects to the idea that duplications may be the source of new genes on the grounds that a gene always influences the same character, whether in a mutant or normal state. However, it may be that a gene is normally limited in its effect only because there is no other gene to take over its function. If a gene locus is present in two places in the chro-

mosome complement, only one of the two is necessary to maintain a complete set of genes. The extra, or unnecessary, locus would conceivably be free to change its function. A mutation of one of the two genes to a physiologically unrelated form should not be lethal since under this condition no existing biochemical step, or other gene-controlled system, would be left without a controlling gene. That no such case has been observed in the laboratory to date may only mean that the process whereby a gene changes to a new type of gene is slow, with many intermediate small steps involved. The duplicated locus might first mutate to a state in which it no longer influenced the original character and in which, perhaps, it had no special influence on the organism. There should be no selection against such a neutral mutation since the other of the duplicated loci will still exert its normal influence. Once it is no longer needed for a particular function, the freed locus could change in a variety of ways until, by chance, it achieves a composition or configuration that is capable of influencing a different biochemical reaction or even of initiating a new chain of biochemical events As long as such theoretical considerations are plausible, it seems premature to discard the suggestion of Bridges (1938b) that "repeats"—duplicated groups of genes —provide for the origin of new genes. This is particularly true when a naturally occurring mechanism, like the one reported here of a transposition followed by crossingover, can explain the appearance of large "repeats," such as are found as part of the normal genotype in chromosomes derived from natural populations of many species of *Drosophila*.

Summary

Under the influence of a high mutation rate gene previously extracted from a natural population, a sample of 13 independent mutations was obtained which showed a change in the sequence of genes on the X-chromosome of *Drosophila melanogaster*. A study of the salivary gland chromosomes revealed the presence of 12 chromosomal inversions and one transposition.

The distribution of breaks along the chromosome was non-random. In all but one case, one of the breaks occurred in the proximal heterochromatic region. A study of the amount of crossingover in adjacent regions suggests that the breaks in heterochromatin are in several different locations.

A correlation of crossover types in the offspring of the transposition strain with the cytological configuration and expected types revealed that about 13% of the offspring carried a chromosome with a duplication of about one-tenth of the genes. The importance of this is discussed from an evolutionary viewpoint.

The results are interpreted as indicating that in addition to causing gene mutations, mutator genes are also capable of altering the sequence of genes on the chromosome by causing inversions, the nature of which depends probably upon the position of heterochromatin; and of supplying natural populations with genetic material from which genes with fundamentally new effects can evolve without the loss of the original genes.

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A THEORY OF ANGIOSPERM EVOLUTION

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INTRODUCTION

The Cretaceous period, which was transitional from the Mesozoic to the Cenozoic era, is well represented by a succession of fossil floras from both hemispheres. These floras record a change from an Early Cretaceous world dominated by typically Jurassic ferns and gymnosperms, to a Middle Cretaceous landscape in which the angiosperms had become characteristic and world wide in distribution. This transformation of vegetation brings us face to face with a major problem: that of early angiosperm evolution. The problem has several facets, which may be viewed in terms of the following questions: (1) What were their ancestors? (2) What is their antiquity? (3) What was the general nature and area of the environment in which they originated? (4) Did they actually assume dominance with "bewildering suddenness" during the Cretaceous? Despite renewed interest, attested by the observations and inferences of numerous writers during the past few years (e.g., Arnold, 1947; Bailey, 1948; Camp, 1947; Chaney, 1947; Just, 1947, 1948; Mason, 1947, Stebbins, 1950; Suessenguth, 1950; Thomas, 1947; Whitehouse, 1950), these fundamental questions have not been satisfactorily answered. Additional data have been presented, but to judge from the diversity of conclusions which have appeared, the solution might seem no more certain today than when Darwin (1879, pp. 20–22), in writing to Hooker, referred to the problem of early angiosperm evolution as "an abominable mystery."

Answers might be found more readily if the ancestral group or groups were known within the gymnosperms, or if, within the record of the angiosperm themselves there were fossils which pointed to these groups. But it is now generally conceded that no known type, fossil or living, can fill this key position. Furthermore, there is almost no fossil evidence by which to evaluate the assumptions of phylogeny which have been based on present morphology. The fossil record does not demonstrate whether the primitive flower was generally of a magnolian type, with spiral arrangement of parts and indefiniteness of number, or whether the simple type of the Amentiferae (oak, willow, alder) comes nearer to the proangiosperms.[1] There is no fossil evidence as to whether monocotyledons and dicotyledons are monophyletic or polyphyletic, or whether the dicotyledons may be in part polyphyletic. The record has thrown almost no light on diverse theories regarding relations within the wider (order) or the narrower (family, genera) alliances.

The fossil record probably never will throw much light, either on the immediate ancestors of angiosperms or their paths of early evolution. The basic types had already evolved by the time angiosperms appear abundantly in the record and, for reasons which will appear, these early types are lost irretrievably. For the present, therefore, we must look primarily to the systematists and morphologists who, by careful, tedious and time-consuming comparisons, no less than by judicious inferences, are now bringing us nearer an understanding of this complex

[1] After reviewing the reproductive structures of megaphyllous seed plants from the Paleozoic and Mesozoic, Thomas (1936, p. 405) concluded: "None of the evolutionary schemes hitherto proposed for the dicotyledons seems to agree with the historical evidence which, moreover, gives no support to the current interpretation of floral morphology."

group. Whilst their researches are more likely to disclose traces of phylogeny than the record of the rocks, there are nonetheless in hand sufficient data to infer the antiquity, the environments of early evolution, and the supposed rapid rise to dominance of the angiosperm phylum. The purpose of the present paper is to clarify these issues in the hope that their proper understanding may give us a broader and clearer perspective in which to view phylogeny, and thus bring us nearer an acceptable explanation of angiosperm evolution.

Angiosperm Antiquity

Mesozoic angiosperms

The character of the known Mesozoic angiosperms supports the belief that the phylum had a long history prior to its assumption of dominance in the Middle Cretaceous. The oldest known plants that conceivably might represent angiosperms are Late Triassic in age. *Furcula* is a leaf fossil from Greenland which, in details of shape, venation and stomata, appears to have all the characters of an angiosperm (Harris, 1932). It probably would have been identified as *Sterculia* or some similar genus had it been collected from Cretaceous or younger rocks. Thomas (1936, p. 404; 1947, p. 251) reports the occurrence of structures (still undescribed) in South Africa which "can be compared only with an inflorescence bearing flowers." One of these has "a whorled perianth of five (or possibly six) segments and a short or disc-like receptacle." These probable angiosperms of early Mesozoic age assume significance in view of the fact that the time from the Late Triassic to the stage of angiosperm dominance in the Middle Cretaceous represents a span of approximately 60 million years (fig. 1).[2]

Angiosperms have been reported from several localities in rocks of Jurassic age. Pollen closely resembling that of modern genera of water lilies, such as *Castalia* and *Nelumbium,* and pollen possibly repre-

[2] The time estimates used here and elsewhere in this paper are taken from Holmes (1947) and Knopf (1949).

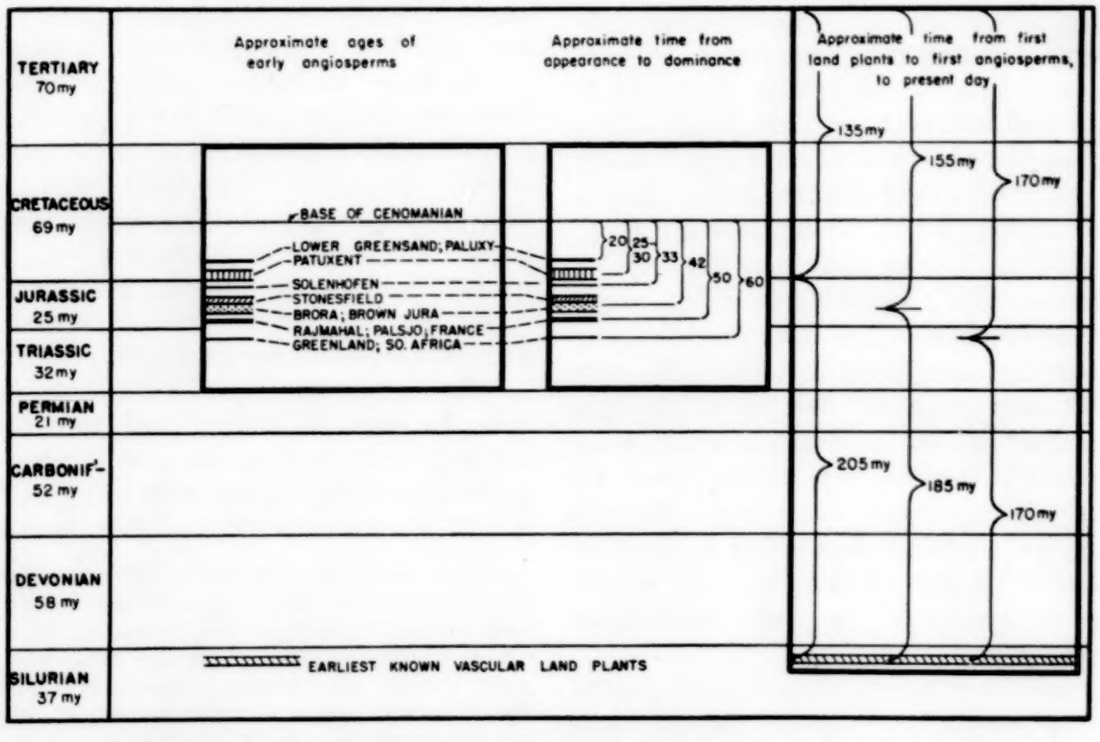

Fig. 1. Showing geologic occurrence of early angiosperms, and approximate time (in millions of years) to angiosperm dominance.

senting *Magnolia,* have been recorded from the Brora coal of Middle Jurassic (Bathonian) age in Scotland (Simpson, 1937). Pollen very similar to that produced by *Eucommia,* of the monotypic family Eucommiaceae of eastern Asia, has been reported from the Early Jurassic shale at Palsjo in northwestern Scania (Erdtmann, 1948). The wood of *Homoxylon* from India, which is possibly though not definitely of Early Jurassic age, closely resembles that of such modern homoxylous angiosperms as *Tetracentron* and *Trochodendron* (Sahni, 1932; Bailey and Nast, 1945). A poorly-preserved leaf, which in outline and basic venation appears to fall readily within the range of variation of *Cercidiphyllum,* is known from the Stonesfield Slate of Middle Jurassic (Bathonian) age in England (Seward, 1904). The leaf of *Ungeria* from the Solenhofen beds of Late Jurassic (Portlandian) age in Germany (Salfeld, 1908), although poorly illustrated, seemingly has the general outline and venation of a compound dicotyledonous leaf such as sumac. Fossil wood described as *Suevioxylon* from the Brown Jura of Germany, which is of Middle Jurassic (Bajocian-Bathonian) age, seems definitely to be dicotyledonous, and to have vessels with the ring-pore arrangement (Krausel, 1928). Leaf fossils described from the Early Jurassic (Lias) of France as *Propalmophyllum* (Lignier, 1907) appear to represent the watern-worn hastulas of palm leaves, some of which contain as many as 15 leaf-rays. They would almost certainly have been referred without hesitation to a *Sabal*-like palm had they been collected from Cretaceous or Tertiary rocks.

These records seem to be fairly reliable indications of the existence of angiosperms in the Jurassic, some 40 to 50 million years prior to their assumption of dominance (fig. 1). The types they represent appear rather certainly referable to present day monocotyledonous and dicotyledonous families of primitive floral types.

The presence of numerous and diverse modern families in Middle Cretaceous (Cenomanian) time also suggests a long prior history. Among the many families represented by leaves at this time are:

Aceraceae	Leguminosae
Anacardiaceae	Magnoliaceae
Araceae	Menispermaceae
Araliaceae	Moraceae
Berberidaceae	Myrtaceae
Betulaceae	Nymphaeaceae
Caprifoliaceae	Palmae
Cercidiphyllaceae	Platanaceae
Combretaceae	Proteaceae
Cornaceae	Rhamnaceae
Cyperaceae	Rosaceae
Dilleniaceae	Salicaceae
Dipterocarpaceae	Sapindaceae
Ebenaceae	Sterculiaceae
Euphorbiaceae	Tiliaceae
Fagaceae	Typhaceae
Juglandaceae	Trochodendraceae
Lauraceae	Vitaceae

These provide indisputable evidence of the advanced state of angiosperm evolution at this early date, particularly in view of the fact that modern genera had become established within both primitive and derived groups. This general conclusion is supported strongly by evidence provided by angiosperm woods from the Early Cretaceous (Aptian) rocks of England, for these show "little evidence of any primitive features (Stopes, 1915, p. 260)." One of them (*Woburnia*) resembles the wood of Dipterocarpaceae, a family now limited to the paleotropics, and another genus (*Aptiana*) appears to represent the Ternstroemiaceae (Scott, 1924, p. 55), also tropical in present distribution. As Seward remarks (1931, p. 400):

> "These stems . . . afford no better clue to the ancestry of flowering plants than we find in the stems of living genera. In other words, the oldest known samples of petrified wood confirm the conclusion based on . . . leaves, that the oldest dicotyledons which clearly reveal their kinship with flowering plants are old only in a geological sense and astonishingly modern in their anatomical features. They confirm our belief in the antiquity of angiosperms antedating by many millions of years, probably several geological periods, the first appearance of the recognizable pioneers of the present ruling dynasty in the modern plant world."

Antiquity

Taking this record at its face value, even though it is incomplete and fragmentary, and even though all the fossils may not be correctly interpreted, the inference seems justified that angiosperms had attained a considerable diversity of floral type by Jurassic time. Other authors have come to a similar conclusion. For example, Stebbins (1950, pp. 501–502) argues that the presence of such derived families as Compositae and Gramineae in the Late Cretaceous probably means that the group is no younger than Jurassic in age. On the basis of the morphological evidence of Cretaceous angiosperms, Camp (1947, p. 181) has suggested that the angiosperm phylum may have come into existence by the end of the Paleozoic, and that divergences of basic generalized family types had been completed by the Jurassic. Thomas (1947, pp. 252–253) points out that since angiosperm evolution seems to have progressed at a rather slow rate once the main groups were established, "it seems reasonable to suppose that the group as a whole could scarcely have originated at a more recent period than the end of the Paleozoic." In this connection, Thomas (1947, pp. 247–248) also recalls that seed plants existed during Permo-Carboniferous time whose leaf characters (simple, entire-margin, reticulate-veined) were not far removed from angiosperms, and further, that cupules like those of the Triassic Caytoniales which rather closely approach the condition of angiospermy, may have existed in the ancestors of angiosperms.

All of this evidence, direct and indirect, points strongly to the existence of angiosperms in pre-Jurassic time. Is there a way by which we can decide on a reasonable bracket of time during which early basic angiosperm evolution may have occurred? The solution to this problem lies, at least in part, in our answer to these alternate questions, namely: did they differentiate from some proangiosperm stock just before their earliest appearance in the record, or did they have their origin at a still earlier date? In the former circumstance they must have evolved so rapidly that they were able to assume dominance during Cretaceous time with an almost modern diversity of type; in the latter they may have evolved gradually but in areas for which there are no records to illustrate their progress.

Data have been assembled in recent years which indicate that evolution may progress rapidly, even explosively, during the initial phases of a phylum and slowly or imperceptibly during its later stages (Simpson, 1944; Stebbins, 1950). This may have been true of the angiosperms. They may have had their origin in earliest Jurassic time, or perhaps Late Triassic, evolving with corresponding rapidity. But if we make this assumption, then we must believe that the diversification required to reach the apparently modern types which had come into existence during the Jurassic occurred within a span of 10 to 15 million years. If so, angiosperms are a unique group among plants, for no other phylum differentiated so rapidly.

The ferns, whose history is best known, appear to have evolved gradually from primitive, ancestral types during much of the Devonian. The ancestors of primitive but modern fern families that evolved from the ancient coenopterids made their appearance in the record only after much of the succeeding Carboniferous period had elapsed. The cycadophytes, which are generally acknowledged to have had their source in Carboniferous seed ferns, probably took most of that period to diverge from a basic seed fern stock of Early Carboniferous age. Cycadophytes are first recorded as rare fossils in the Late Pennsylvanian and are not prominent until the Late Permian and Early Triassic. Conifer history also generally parallels that of ferns and cycadophytes for primitive types were widely spread during the Late Pennsylvanian, while more modern derived types are not commonly encountered in the record until the Triassic.

The record of ferns, cycadophytes and coniferophytes thus shows that ancestral types were abundantly represented in the record several tens of millions of years before the first derivative, or more modern types are recorded in small numbers. In this connection Simpson has earlier pointed out that in the case of vertebrates (1944, p. 110):

> "The ancestral type, at about the time of probable origin, is often well recorded and representative of probably abundant and widespread groups, while the first representatives of the new type are usually rare as fossils. . . . Devonian crossopterygians are now very well known, but their descendants the amphibians are exceedingly rare fossils until the Pennsylvanian, millions of years after this class originated. Then the amphibians are common, but the first reptiles, in the later Pennsylvanian, are rare. Mammal-like reptiles are common Triassic fossils, but only a few fossil mammals are found before the Paleocene. . . ."

If the history of ferns, cycadophytes and coniferophytes is analagous with that of the angiosperms, and if plant evolution has generally paralleled that of animals with respect to tempo and mode, as appears to be the case (Stebbins, 1950), then we may well infer that angiosperms had a long history before they were first recorded. One may argue that angiosperms are a unique group, and that they have exceeded these other groups in rate of evolution. But this is an assumption—previously accepted by most authorities—for which there appears to be no supporting evidence. Actually, to judge from the probable angiosperms of Late Triassic age and from the occurrence of apparently modern family types in the Early and Middle Jurassic, it seems reasonably certain that angiosperms had advanced well beyond the proangiosperm level by Late Triassic time. This leads to the possibility, at least, that they had their origin during Permian or Permo-Triassic time, some 40 to 50 million years prior to the first fragmentary records of Jurassic angiosperms—a conclusion which has been reached earlier by Camp and Thomas. If this is true, then we may well ask: Where were these angiosperms and why do we have no Permo-Triassic records of them?

Site of Early Evolution

The belief has been expressed by most investigators that early angiosperm evolution took place in upland regions, in areas sufficiently removed from the usual lowland basins of deposition to have precluded their occurrence as contemporaries in the fossil record. This explanation appears to be a rather lame one, principally because sound reasons for selecting such a site generally have not been given (e.g., Arnold, 1947, p. 334; Berry, 1945, p. 89; Seward, 1931, p. 366). Actually, there are 3 lines of evidence which give strong support to the thesis of early angiosperm evolution in upland areas.

Environments represented by fossil floras

Ecological studies of living and, by inference, of fossil plants have demonstrated that the plants which make up the bulk of the record have been those which lived at or close to the site of deposition (e.g., Chaney, 1938a). During most of geologic time these sites have been typically on the broad floodplains of lowland valleys, on lake margins, on deltas, and in estuarine or lagoonal habitats—the regions where most of the sediments which make up the continental record have accumulated. There are, of course, records of upland floras, notably those which accumulated in mountain lakes. But it must be emphasized that such deposits, like those at Creede in Colorado (Knowlton, 1923) or at Liddarmarg in northern India (Puri, 1947), are recent in a geological sense. As we go further back in Tertiary time, we encounter fewer and fewer sediments which were laid down in highland basins. They are exceedingly rare in the Early Tertiary and are hardly represented at all in the rocks of earlier periods. This is due to the fact that upland deposits rarely can persist very long

in the geological record. Mountainous and upland areas are continually subject to denudation, and those sediments which do accumulate are among the first to be destroyed.[3] Furthermore, sediments laid down in highland regions are confined to small, local basins of deposition, in contrast to the extensive formations which are usually built up over the broad floodplain, delta, and estuarine sites of lowland regions. Localized upland deposits would therefore have still less chance of surviving for any long period of time, though rarely they might be expected in structurally complex regions. To be preserved through several periods of geologic time, continental sediments and their entombed fossils almost necessarily must be laid down at or near sea level, and then be buried by younger sediments or lavas, or be depressed below base level, so that they are removed from the processes of weathering and erosion. Almost exclusively, therefore, the older floras are representative of lowland vegetation and the record is correspondingly biased since the upland floras of the same period, the Triassic or Jurassic for example, have largely been lost. This is a bias in favor of lowland floras, and one which increases the further back in time one goes. Hence in the earlier periods it tells us nothing about the upland floras which may then, just as now, have included a much greater diversity of type than did those floras bordering the lowland sites of deposition. Thus the absence of Permo-Triassic records of angiosperms is not surprising, but is fully consistent with the thesis that they may have evolved in upland regions of that period.

Inferences from cliseres

A clisere represents a succession of vegetation types (plant formations, or climaxes) which supercede one another in an area as a result of changing environment during the course of time. Wherever successions of floras have been studied, whether of Paleozoic, Mesozoic or Cenozoic age, cliseral relations demonstrate that plants of generally higher and more specialized type, and also of most recent appearance in the lowland environments, have appeared first in uplands of the region long before they entered the lowland record to replace the older flora. From the numerous examples that demonstrate these relationships, we refer briefly to the following.

1. Middle Devonian gymnosperms (*Paleopitys, Callixylon, Dadoxylon*) of relatively high organization included trees with thick trunks. Evidence of weathering and battering of the stems indicates their transport from more distant uplands to sea level, where they are found associated with the ancient and simple psilophytes. Gymnosperms are not recorded as common and established in lowland vegetation until the end of the period.

2. A succession of 24 floras of Pennsylvania and Permian age in Kansas shows that "typical Permian fossils" invaded the lowlands there during a drier stage in the Late Pennsylvanian, disappeared there when the climatic trend showed a temporary reversal to more humid conditions, and reappeared when the Permian environment was favorable for them (Elias, 1936). During the humid interval (and earlier) they were restricted to the drier and more distant upland slopes.

3. Temperate forests representing the Arcto-Tertiary Flora existed in the uplands at middle latitudes during Eocene time, when lowland floras were almost wholly tropical to subtropical. As temperatures were gradually lowered following the Eocene, the Arcto-Tertiary Flora invaded the lowlands and had largely displaced the older tropical vegetation by the end of the Oligocene (e.g., *Green River flora,* Brown, 1934; Wodehouse, 1932, 1933; *Clarno flora,* Chaney, 1938b;

[3] Recent estimates indicate that if current rates of denudation were maintained, and not compensated by upward movement of the crustal region, all the land area could be eroded to sea level in about 23 million years (Gilluly *et al.*, 1951).

Wilcox flora, Brown, 1944; *London Clay flora,* Reid & Chandler, 1933).

4. Semiarid plants comprising the Madro-Tertiary Flora occupied the lower to middle slopes of the Sierra Nevada during Late Miocene time (Axelrod, 1938, 1939; Condit, 1944a, 1944b). Contemporaneous floras living at sea level in the San Francisco Bay region 60 miles westward were temperate and mesic in character, and the semiarid Madro-Tertiary species have not been recorded among them (Condit, 1938). A succession of 8 Pliocene floras in the coastal region shows Madro-Tertiary plants gradually invading that area as rainfall decreased, and largely displacing the mesic flora by Middle Pliocene time (Axelrod, 1944).

Evidence from cliseral relations lends strong support to the belief that plants have occurred in upland sites long before entering the accumulating sediments in the lowlands to become an important part of the floras recorded. Plant fossils from sediments of the lowland sites which make up most of the record can give us only a little information on vegetation of the bordering hills, and almost no data on plants living in more distant upland regions. Since the few Jurassic angiosperms in the fossil record are wholly subordinate to the lowland vegetation of ferns and gymnosperms, the possibility does exist that they represent subordinate members of that vegetation. However, there is no unequivocal evidence to support such a view. On the contrary, a study of cliseres makes it seem much more likely that these angiosperms of rare occurrence in the Jurassic record were representatives of a vegetation which occupied upland environments far removed from those which have been preserved. Such a site for early angiosperm evolution assumes considerable significance since there is a greater likelihood that a new adaptive type would become established in the uplands than in the more equable environments of the lowlands bordering sites of deposition.

Conditions for the origin of new adaptive types

Certain conditions are necessary for the establishment of a new adaptive type (Simpson, 1944; Stebbins, 1950). Most important of the external conditions is the existence of a variable environment (physical and biotic), for diversity of environment tends strongly to promote rapid evolution and probably is essential to it. Among the prime biological conditions necessary in the ancestral type are the presence of a high degree of heterozygosity, the occurrence of characteristics (physiological and morphological) which are preadaptive in the directions of change, and a favorable population structure.

Diversity of environment plays a dual role. In the first place, many more adaptive types—vegetative as well as floral—can be accommodated in a diversified as compared with a more homogeneous environment. Since selection can play on a wider variety of potentially adaptive types in a complex physical and biotic environment, many more evolutionary patterns are possible in regions of environmental diversity. In the second place, diversity of environment tends to promote the subdivision of a species into discrete groups. The fragmentation of a species into local breeding groups of generally small size is favorable for rapid evolution. Such a population structure enables new gene combinations to become established which are not subject to the swamping effects which commonly occur in large populations. By the accumulation of different genes in these small, discrete units there is a corresponding genetic diversification of the whole. The subdivision of a species into local groups of restricted size also increases the probability that latent preadaptive characters may become expressed in these smaller units. The recombination of two or more of these divergent types may result in the development of a potentially new adaptive type. Nevertheless, a prime requirement is the occurrence of an environment with which the

adaptive type is potentially in harmony and within which it may be expressed. Given such an environment, the potential may become realized and the type established locally. The shift from one adaptive type to another may be abrupt and may be of considerable magnitude, dependent on the genotype expressed and the degree of environmental difference with which it reacts. Since the uplands are characterized by relatively large and abrupt environmental differences, the probability is higher that new adaptive types will tend to develop first in upland areas than in the lowlands. During the initial and early evolution in such areas, when a group would be represented by generally small populations, its chances for entombment at this time in the lowland record would be greatly reduced in comparison with a later period in its history when large populations would exist.

Thus our inferences regarding site of early angiosperm evolution, as indicated by the nature of upland deposits in time and by the cliseral relations of vegetation, are reinforced strongly by the increased probability that the diversity of environments in such areas would more likely result in the successful evolution of a new adaptive type. Since highland sites can be preserved only rarely (if it all) in the older geologic record, and since angiosperms probably were evolving in these areas as relatively small populations, it is not surprising to find the earliest angiosperms are still unknown in the record. There is every reason to suppose that we may never find their megascopic remains, or at least that they will always be among the rarest of fossils.

Environments of Early Angiosperm Evolution

The evidence and arguments set forth in the preceding section suggest that the origin and initial diversification of angiosperms, as now represented by ordinal and family types, might have occurred in upland environments during Permo-Triassic time, long before the phylum appeared in the fossil record. The effect of remoteness from lowland sites of deposition would be to make the inclusion of angiosperms in the sedimentary record most unlikely, whilst the presence of diversified environments in the uplands would tend to encourage both the origin of the type and its initial diversification there rather than in the more equable and homogeneous environments of the lowlands. Should this have been true, then we may well enquire as to the general nature of the environment under which early angiosperms evolved. Did the early evolution of the angiosperms take place in temperate holarctica, in austral regions, or does the ancient tropical world represent the area of primary diversification? This is a critical question. It holds the key to an understanding of basic early angiosperm evolution following the initial appearance of the group (or groups, if angiosperms are polyphyletic) irrespective of the actual time (Permo-Triassic or other) of first appearance in the uplands. The answer to this question must concern fundamentally any theory of early angiosperm evolution, for not only has evolution at any given time always depended on the interaction between hereditary variations present in the population and the environment in which the population lived, but during the long course of geologic time climate appears to have had a major role in directing plant evolution.

Unlike most land animals, plants are rooted or fixed to their environment. The combination of water and temperature relations, modified as they are by edaphic factors, exert a primary control on both their existence and persistence within any given area. Major trends of climatic change during long spans of geologic time will therefore be of highest significance to plant evolution for the appearance and expansion of new climates will make possible the development within a phylum of many adaptive types which otherwise could not have appeared and persisted. Granting that genetic diver-

sity must always be present in evolving lineages, and that selection is a major factor in the evolution of more highly adapted types in any environment, then it must follow that new adaptive types, such as those represented by plants of desert, thorn scrub, tundra or chaparral communities—all of which comprise a wide range of family floral types—have evolved as the climates to which their antecedents responded gradually changed. It would appear axiomatic that for desert plants to evolve a desert climate is needed, and that tundra plants scarcely can differentiate in a tropical rain forest environment. If the environments of Paleocene time had remained largely unchanged down to the present day, the words desert and tundra probably would not be in our vocabulary, for their present areas would still be occupied largely by derived types of temperate (Arcto-Tertiary, Antarcto-Tertiary Floras) and tropical forests (Neotropical-Tertiary, Paleotropical-Tertiary Floras).

The notion that the general course of plant evolution has been directed largely by climate is not a new one. It has been exploited by the geologist Andrews (1913; 1914) in his skillful analysis of the Myrtaceae and Leguminosae, as well as by the botanist Bews in his critical essay on the ecological evolution of angiosperms (1927). The idea developed by Andrews is, in brief, that equable climates have tended to produce widely ranging floras, whilst differentiation of climates has resulted in their localization. A trend toward increasing diversity of climate would "tend to produce marked local variation . . . and thus an erstwhile widespread type would . . . tend to contract its range altogether as regards the primitive type, . . . while local types would arise as the result of adaptation to new environments . . . (1913, p. 548)." Applying this idea to the problem of early angiosperm evolution we might suppose that (a) the more ancient and primitive groups, as represented now by ordinal and family (or subfamily) categories, might well be in environments generally like those of the ancestral type, and that (b) the more highly evolved types of each alliance might be found in more specialized environments. To ascertain what relation this thesis may have to the environments of initial angiosperm diversification, we shall enquire briefly into first, the adaptive character of the most primitive living angiosperms, and second, that of the phylum as a whole.

Adaptive character of primitive angiosperm types

The magnolian alliance (Annonales, Laurales, Magnoliales) is generally conceded to represent the most primitive angiosperm type now extant, with the Annonaceae probably representing its most generalized form. As shown in figure 2, the alliance is at present predominantly a part of the plant communities of the tropics. Most of the group is primarily found in tropical forests and the larger families and most of the genera are concentrated there. Less than 10 per cent of the 200-odd genera in the group belong to temperate communities. The alliance shows 5 basic patterns in distribution which express the adaptedness of the group, as shown in table 1. The genera of a given family which depart most widely from floral type are found most frequently in communities of drier and cooler aspect which immediately border the tropical forests, or else they occur in the warm temperate to temperate forests adjacent to the tropics at higher latitudes. Likewise, the relictual monotypic families which depart most widely from type are also found in the extratropical areas. Thus the most primitive living angiosperm alliance now seems to be primarily adapted to the equable and wet forests of the tropics, and secondarily adapted to the related subtropical, warm temperate and temperate forests which border them, a fact which has been noted earlier by Bews (1927, pp. 72–73).

Evidence indicates that these present

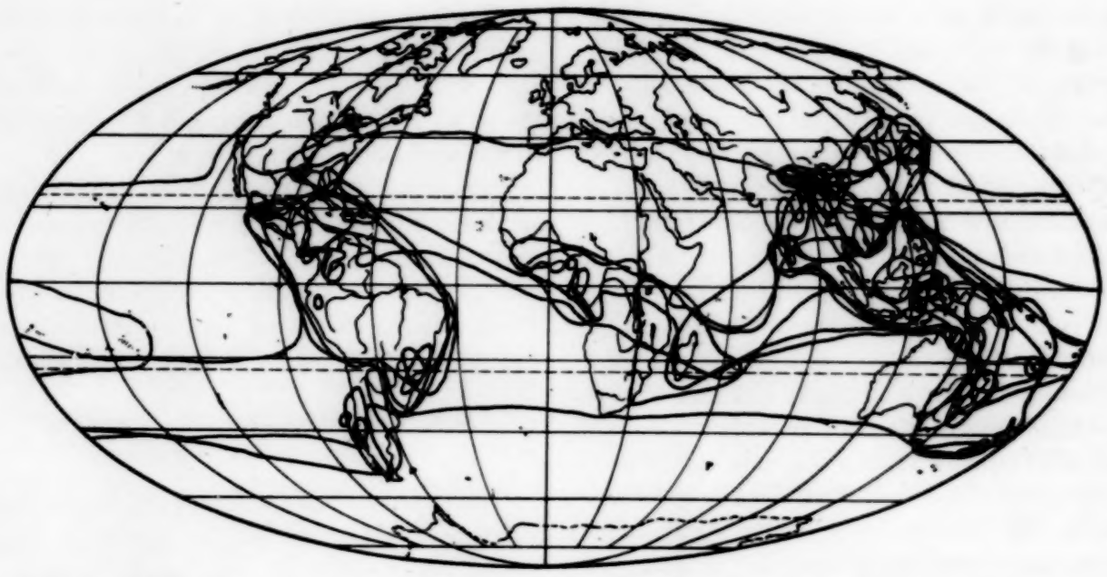

FIG. 2. Distribution of the primitive magnolian alliance. In this and succeeding figures (figs. 3–9) distributional data for the families have been compiled from maps drawn by Good (1947), Hutchinson (1926; 1934) and Vester (1940).

conditions reflect those of the early evolution of the alliance, and that the tropical regions in which the group underwent its evolution were much more widespread than now. A survey of climates during geological time shows that the tropical to warm temperate zone occupied a considerably broader zone during most of the geologic past than at present. From the Middle Cretaceous to the Oligocene, a span of approximately 70 million years, this zone included a region whose northern and southern borders generally ranged from 45° to 55° N and S latitude. Wherever genera of the magnolian alliance have been recorded in floras during this long interval they have been associated regularly with tropical to warm temperate environments, whether the floras be from Alaska, Great Britain, California, Japan, New Zealand, or southern Argentina.[4]

With respect to the Jurassic fossils which appear to represent the magnolian alliance (pages 30–31), analysis of the biota clearly supports the idea of warm and equable climates extending over the lowlands, with subtropical conditions ranging probably as far N and S as 50° during this period, as well as in the Late Triassic. Plants included in the lowland floras during this interval include such adaptive types as tree ferns and filmy ferns which could scarcely have existed under any other conditions than those of moist forest, whilst the occurrence of forests within the arctic and antarctic circles (*see* Seward, 1931, figs. 103, 104) demonstrates the existence of equable climates over wide areas. The marine invertebrate faunas of this period also provide strong evidence for warm tropical waters at higher latitudes. The fact that the marine faunas and the continental floras were similar in composition over wide areas must mean also that localized environments could not have been prominently developed during most of the period, and that equable conditions prevailed over most of the earth's surface.

While the lowland climates were chiefly tropical to warm temperate through much of the region between latitudes 50° N and S, with more temperate environments at higher latitudes and savanna conditions at

[4] In this connection it is pertinent that some of the derived genera of the group that now occur largely in temperate areas (*Liriodendron, Cercidiphyllum, Sassafras*) were regularly found with subtropical to warm temperate forests during the Late Cretaceous and Early Tertiary. (See page 52.)

middle latitudes on the western sides of the continents, we do not know what lay in the uplands where the Jurassic angiosperms are thought to have been in existence. We can suppose by analogy with modern environments that within the wide tropical zone humid forests extended well up the mountain slopes, giving way gradually to more temperate environments at higher levels, with local subhumid areas to the lee of the higher, more continuous mountain ranges.

The evidence seems to indicate that the most primitive angiosperm type is adapted to equable environments of tropical forest and has largely been since its origin. As judged from the data summarized in table 1, the group has exploited tropical regions primarily, but has shown a tendency also to range into the boreal or austral regions marginal to the tropics, whilst the more derivative types have differentiated into the warm temperate and temperate forests marginal to the tropics. On this basis we may infer that (1) primitive angiosperms of tropical distribution gave rise to numerous basic evolutionary types adapted to tropical regions; that (2) some of the latter groups have exploited tropical environments chiefly, and that (3) some of them, as well as their derivatives, have also contributed types adapted to the extratropical environments as well. In other words, should these inferences be correct, at least in broadest and simplest terms, then we might expect the angiosperm phylum as a whole might show that it is basically adapted to tropical regions, with derivative types in both tropical and extratropical environments.

Adaptive character of the angiosperm phylum

The pattern of adaptedness seen in the magnolian alliance is reflected on a grand scale throughout the whole phylum, as Bews has shown (1927). The facts of present occurrence and of departure from type of families within orders, and of genera within families, taken in relation to their present and past environments, strongly indicates first, that the phylum as a whole is basically adapted to equable environments, second, that it spread widely over the earth when such environ-

TABLE 1. *Showing (a) most of the primitive angiosperm families are primarily adapted to tropical environments, and (b) the basic patterns in distribution of the magnolian alliance. (Approximate number of genera in families shown in parenthesis)*

		Total genera (approximate)
1. Tropical, including families that are either:		
a. Pantropic. Annonaceae (76), Hernandiaceae (4), Myristicaceae (16)	97	97
b. Discontinuous in tropics (none recognized)		
c. Endemic in tropics. Degneriaceae (1)		
2. Tropical chiefly, with some genera ranging into *both* northern and southern temperate and drier regions. Lauraceae (48)	48	
3. Tropical chiefly, ranging into cooler and drier austral regions. Eupomatiaceae (1), Himantandraceae (1), Monimiaceae (30), Winteraceae (6)	38	99
4. Tropical chiefly, ranging into northern temperate regions. Illiciaceae (1), Magnoliaceae (10), Schizandraceae (2)	13	
5. Extratropical in distribution.		
a. Warm temperate to temperate in northern regions. Cercidiphyllaceae (1), Eupteleaceae (1), Trochodendraceae (2)	4	6
b. Warm temperate to temperate in southern regions. Gomortegaceae (1), Lactoridaceae (1)	2	

ments were widespread, and third, that most differentiation from the basic tropical types has been within the tropics, with secondary evolution in the less favorable or more specialized environments of the tropical and extratropical regions. This idea, which has been exploited by Andrews (1914, 1915) and Bews (1927), would not preclude the later return to a more mesic climate on the part of some components of a type which had become adapted, at least in part, to a less favorable environment (Stebbins, 1952).

The facts that bear on the present thesis are so numerous and so intricately related that their exploitation in full would require several volumes. The data for evaluation lie in the scores of monographs and shorter papers treating the various genera, families and orders, whether the point of view be taxonomic, morphologic, genetic or paleontologic, as well as in the contributions to ecology and distribution. The large body of basic information assembled by Bews (1927, *esp.* pp. 67–84, 129–148) strongly supports the thesis. Although his examples could be greatly extended on the basis of more recent researches, my purpose here is only to outline again Bews' solution of the problem, and not to marshall additional evidence which would more fully document and substantiate the idea.

Bews' brief yet pertinent review of the adaptive trends in the orders, families, subfamilies, tribes and genera of flowering plants illustrates in alliance after alliance that the trends of diversification in flower and fruit on which phylogeny is largely based, correspond to trends in diversification of growth form which express different environments, and further, that the more primitive floral types of a given alliance more frequently than not are associated with tropical environments, and the derived types with the more specialized tropical and extratropical environments. There appears to be no doubt that the basic pattern of adaptedness displayed by the primitive living angiosperms can be clearly seen throughout the whole phylum. As Bews points out (1927, pp. 6–10), some family types have maintained a similar adaptive character for long periods of time. For example, such families of Dipterocarpaceae, Ebenaceae, Lauraceae (Persoidae), Magnoliaceae, Palmae, Rhizophoraceae and others have been a component primarily of tropical forests since the mid-Cretaceous (if not longer). They show only moderate adaptive diversity in the tropics and have scarcely exploited the extratropical regions. Others, while largely tropical, have nonetheless become highly diverse in adaptive character within the tropics, where they are represented by trees, shrubs and climbers or herbs (e.g., Annonaceae, Apocynaceae, Dilleniaceae, Gesneriaceae, Hippocrateaceae, Malpighiaceae, Melastomaceae, Ochnaceae, Olacaceae, Quiinaceae); the more specialized floral and vegetative forms are frequently in the more specialized or extreme tropical or marginal tropical environments. Some tropical families are represented by specialized plant types only, and often these are more derived members in their respective alliances (e.g., Ancistrocladaceae—scandent shrubs in the Theales; Loranthaceae—largely parasitic shrubs in the Santalales; Turneraceae—largely herbs in the Cistales; Hydnoraceae—root parasites in the Aristolochiales; Marcgraviaceae—climbing and epiphytic shrubs in the Theaceae). Still other families, while largely tropical, are found also in temperate or arid regions, or both (e.g., Anacardiaceae, Bignoniaceae, Burseraceae, Capparidaceae, Euphorbiaceae, Lythraceae, Menispermaceae, Oleaceae, Oxalidaceae, Rubiaceae, Rutaceae, Santalaceae, Sapotaceae, Sterculiaceae). In most cases they are represented in the extratropical regions by more specialized types (species, genera, tribes) in respect to both floral structure and plant form. The families that are now found largely in extratropical regions show similar relationships. Many families of wide distribution find their affinities with primarily tropical groups (e.g., Umbelliferae with the Araliaceae, Gentianaceae with

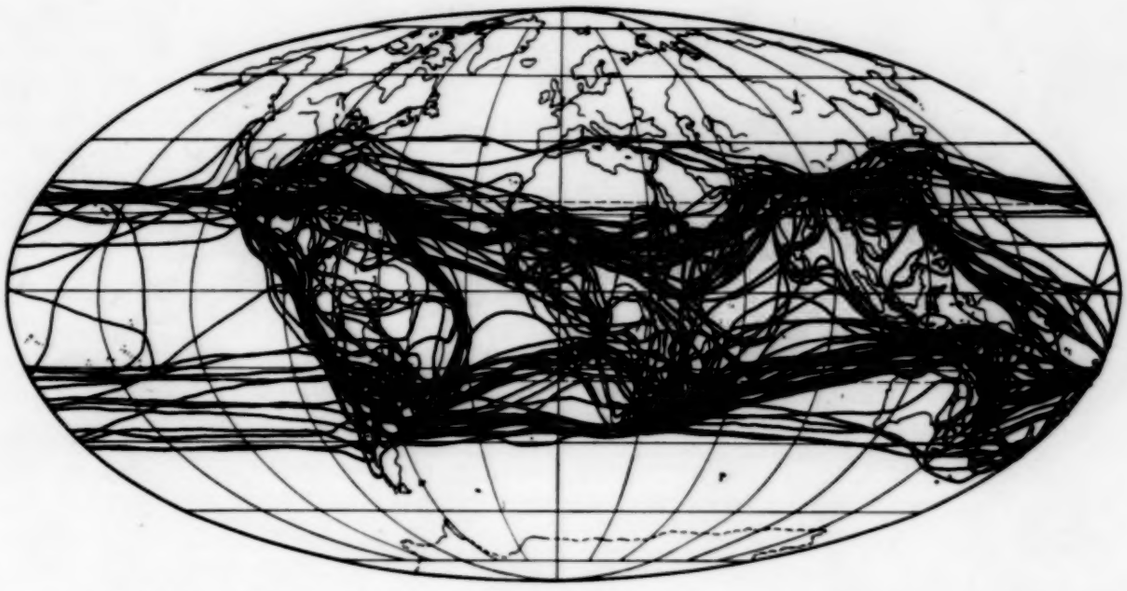

FIG. 3. Distribution of 40 of 54 families that are characteristically pantropic.

the Loganiaceae, Grossulariaceae with the Escalloniaceae, Labiatae with the Verbenaceae, Cruciferae with the Capparidaceae, Primulaceae with the Myrsinaceae, Geraniaceae with the Malpighiaceae-Oxalidaceae, Cannabinaceae with the Moraceae-Urticaceae, Malvaceae with the Bombacaceae, Campanulaceae with the Lobeliaceae). In addition, many of the 40 families that are narrowly confined to the dry and temperate regions (fig. 9) chiefly find their closest relationships in types that are basically tropical (e.g., Koeberliniaceae with Simarubaceae, Julianiaceae with Anacardiaceae, Stachyuraceae with Hamamelidaceae, Myzodendraceae with Santalaceae, Nolanaceae with Solanaceae-Convolvulaceae, Myrothamnaceae with Hamamelidaceae, Phrymaceae with Verbenaceae, Cneoraceae with Simarubaceae-Rutaceae, Actinidiaceae with Dilleniaceae-Theaceae, Eucryphiaceae with Cunoniaceae, Achariaceae with Passifloraceae). The evidence reviewed by Bews

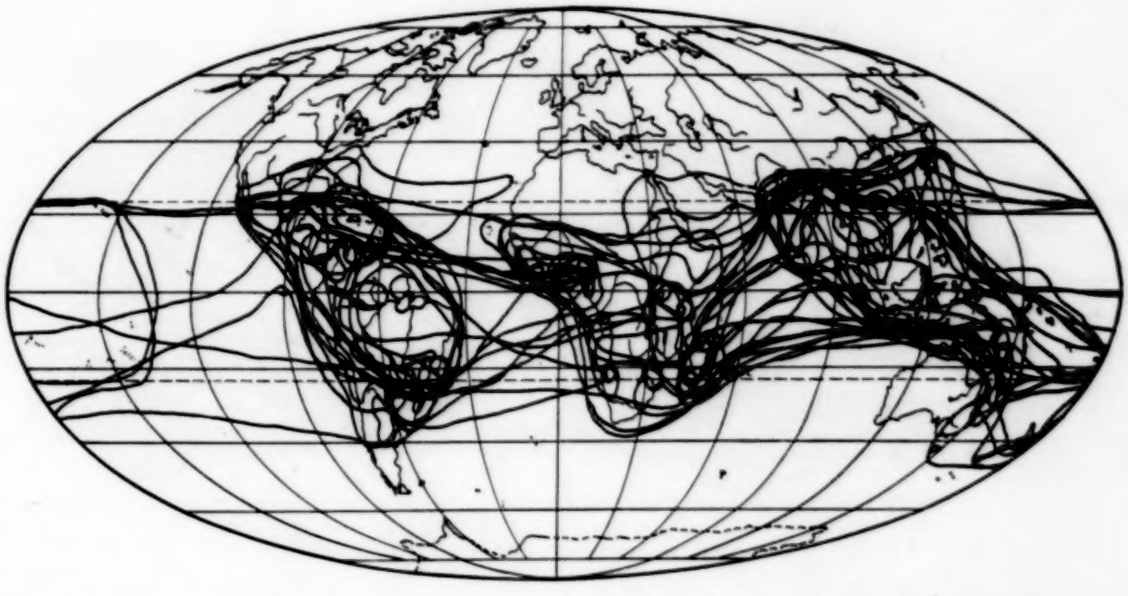

FIG. 4. Distribution of 28 of 41 families that are characteristically tropical, but discontinuous in the tropics.

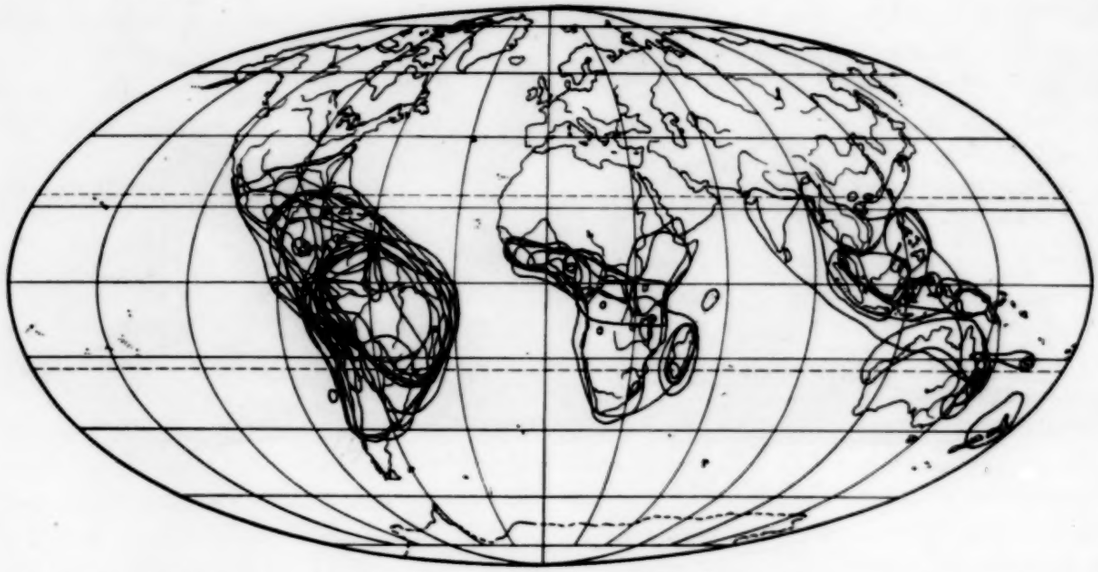

FIG. 5. Distribution of 52 endemic (wide and narrow) families that are characteristically tropical in occurrence.

makes it seem reasonably certain that the phylum was basically adapted to moist tropical forests, and that it has become adapted to the more specialized environments of the tropical and extratropical regions.

These relationships show up clearly on maps which depict the occurrence of angiosperm families in the world environments. The distribution of the 330-odd families of flowering plants has been summarized recently by various authors (e.g., Hutchinson, 1926, 1934; Vester, 1940; Good, 1947). Some of the data which are pertinent to the present topic are presented in figures 3–9, and are summarized in pictorial manner in figure 10. The significant fact to emerge from the present compilation is that one-half of all flowering plant families are characteristically tropical in occurrence (figs. 3–5). Furthermore, if we add to this group

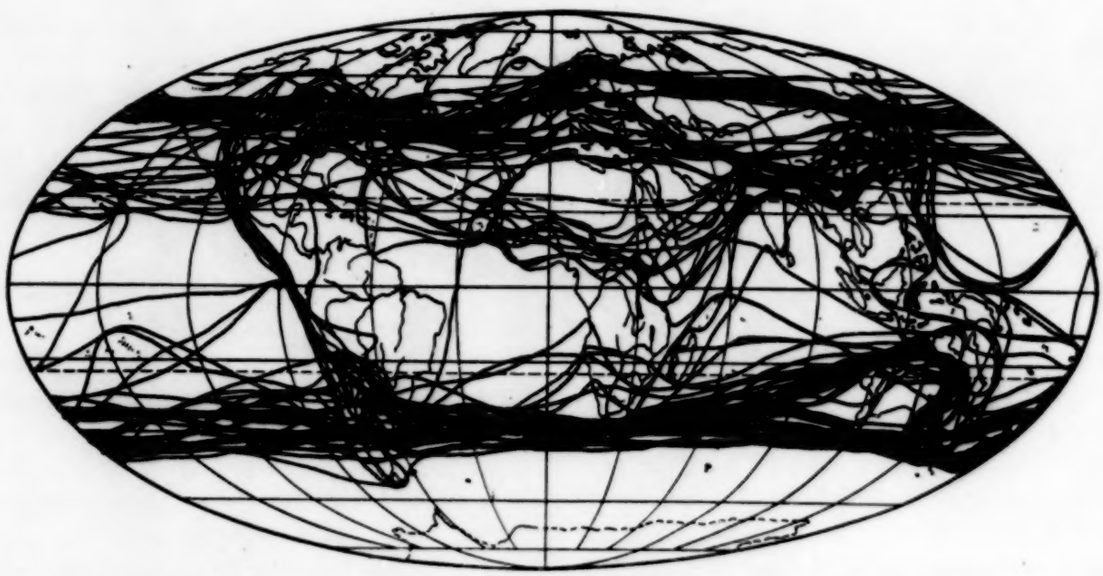

FIG. 6. Distribution of 40 of 77 families that attain optimum development and diversity in the tropics, but which range into northern and southern extratropical regions.

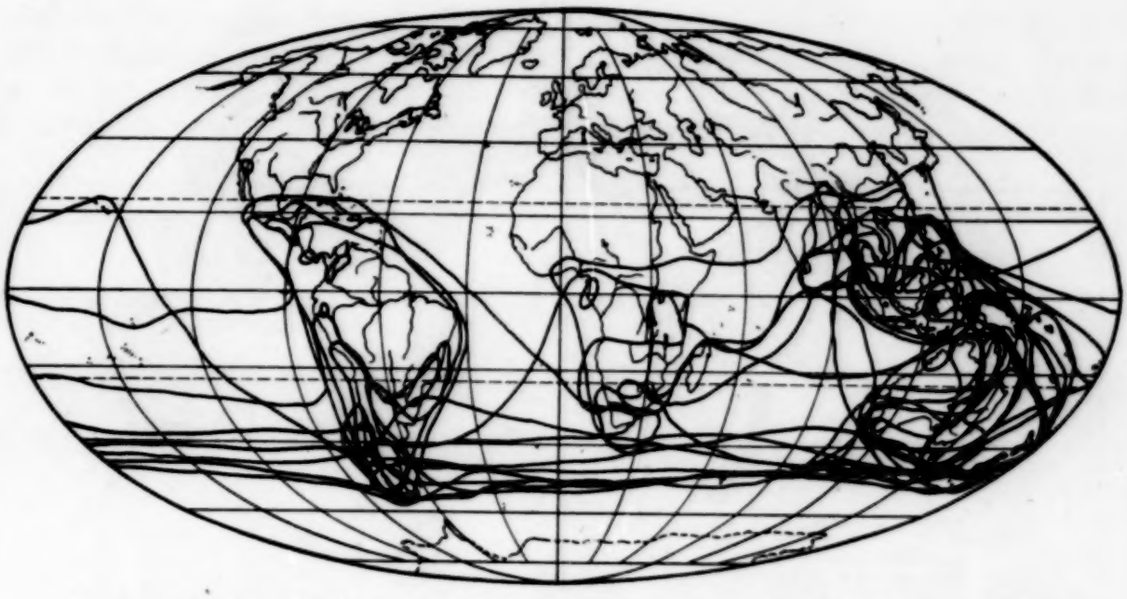

FIG. 7. Distribution of 17 of 22 families ranging from tropics chiefly into southern extratropical regions.

those families which, while attaining optimum development and diversity in tropical regions, also range into extra-tropical areas (figs. 6–8), then fully three fourths of all angiosperm families must be considered as primarily adapted to tropical environments. Most of the remainder, such as the families narrowly confined to extratropical regions (fig. 9), appear to have been derived from families that are largely or wholly tropical.

Thus the evidence from the most primitive living angiosperm families, and from the phylum as a whole, indicates that the group is primarily adapted to tropical environments. Basic tropical types appear to have been contributing derived species, genera and families not only to tropical regions, but to the border tropical environments, as well as to the temperate (holarctic, antarctic, high mountains) and to the drier regions on all

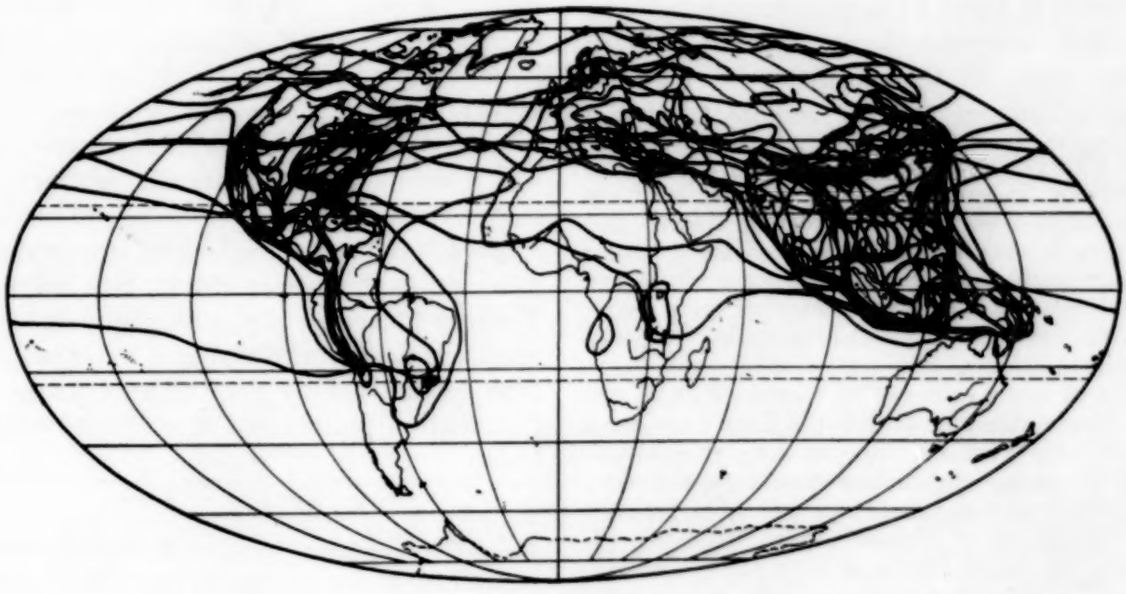

FIG. 8. Distribution of 20 of 22 families ranging from tropics chiefly into northern extratropical regions.

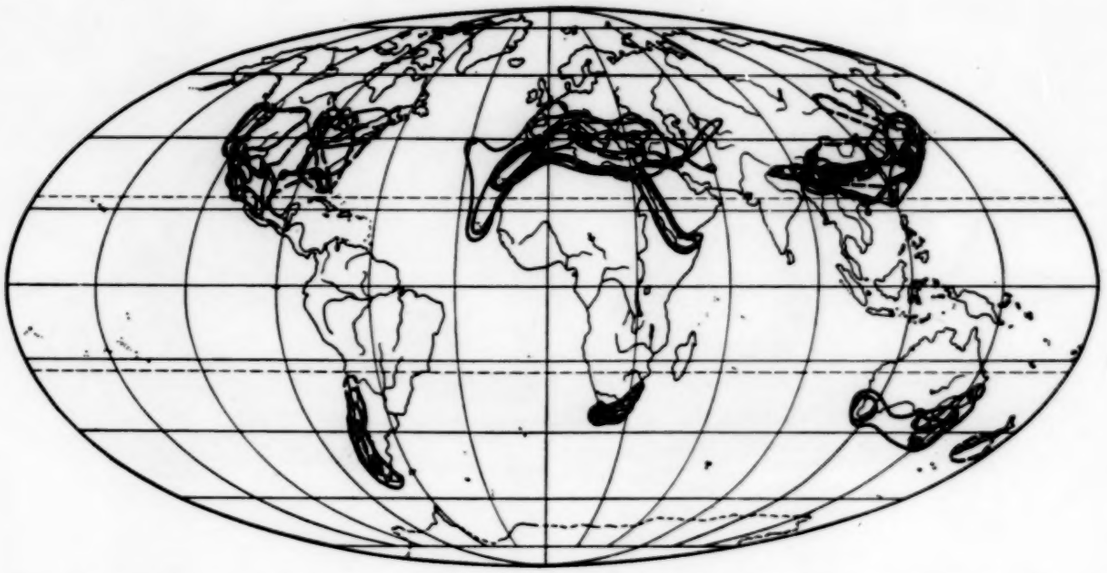

FIG. 9. Distribution of 40 families narrowly endemic (solid lines) or discontinuous (dashed lines) in extratropical regions. Many of them appear to have been derived from families that are primarily adapted to tropical environments.

continents during the long time they have been in existence. This leads to the inference that the earliest angiosperms probably were tropical in distribution, occupying the warm uplands of the pre-Jurassic, possibly Permo-Triassic world.[5]

THE PROGRESSION OF ANGIOSPERM FLORAS

The data which we have been considering up to this point have led to the inferences that (1) angiosperms may have been in existence during Permo-Triassic time, that (2) they probably were evolving in upland regions remote from the lowland sites of deposition which largely make up the older geologic record, and that (3) the tropical uplands probably were the principal reservoir of early, primary angiosperm evolution. By using these inferences, by taking into account the ideas developed by Bews and Andrews with respect to the ecological evolution of angiosperms, and by bringing into consideration the fundamental advances made recently in an understanding of evolution (e.g., Simpson, 1944; Stebbins, 1950), it is possible to make certain additional suggestions regarding early angiosperm evolution. In the following discussion reference is made to figure 11, which shows diagrammatically the various stages visualized in the evolution of angiosperms following their initial appearance from unknown ancestors in the Permo-Triassic tropical upland regions; the world land area outlined is a hypothetical type often used by geographers to show distribution patterns of climate and vegetation.

Pre-Cenozoic Floras

Permo-Triassic. Ancient angiosperms, including types generally foreshadowing present day primitive monocotyledons and dicotyledons are postulated as being in

[5] This evidence for early, primary angiosperm evolution in tropical regions, coupled with the *present day* high concentration of families and genera in the Indomalaysian tropics and border areas, might tempt some investigators to regard that region as the initial "center" of early angiosperm evolution. Paleontological evidence scarcely supports such a view, since many paleotropical types occurred in western Europe and in North America during the Late Cretaceous and Early Tertiary. Furthermore, paleobotanical evidence demonstrates that all the present day tropical floras must be regarded as relictual of earlier, more widespread communities. Finally, the fossil record of both plants and animals clearly demonstrates that present day distributions can not be used as an index to the "center" of evolution of any phylum.

upland regions ranging from tropical to warm temperate in character. As emphasized earlier, upland areas are characterized regularly by greater environmental diversity than usually exists over the lowlands. Furthermore, because Permo-Triassic time was typified by climates which were more extreme than those of

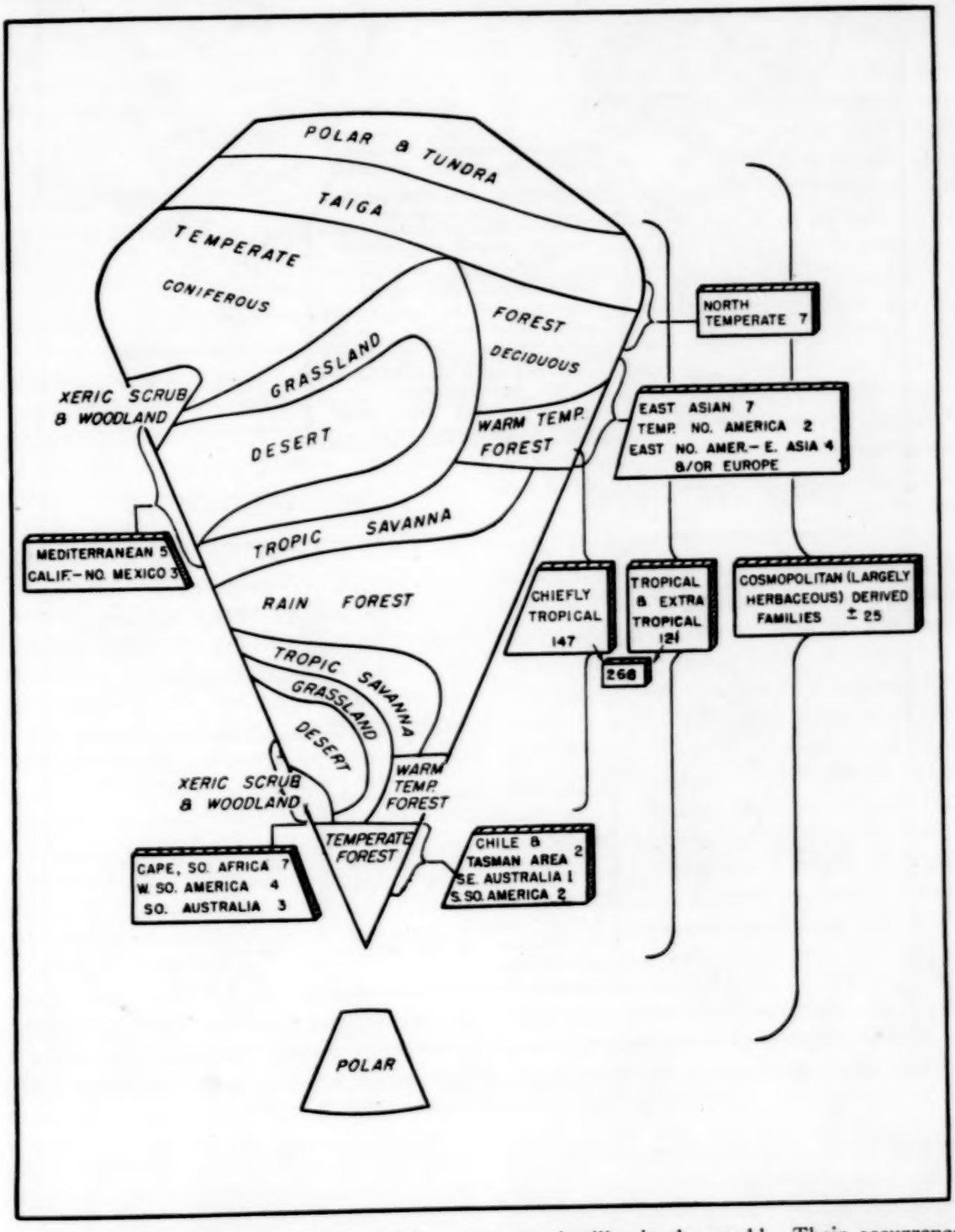

FIG. 10. Showing concentration of 300 angiosperm families in the world. Their occurrence is plotted on an idealized land area of the type often used by geographers to show the distribution patterns of vegetation or climate. In this figure (also in figs. 11, 13, 14) the concentration of land in the northern hemisphere is apparent, as is the isolation of antarctica at the south. Although the same world shape has been used in figures 11, 13, 14, the proportions of land in the hemispheres changed during time, as did the southern connection.

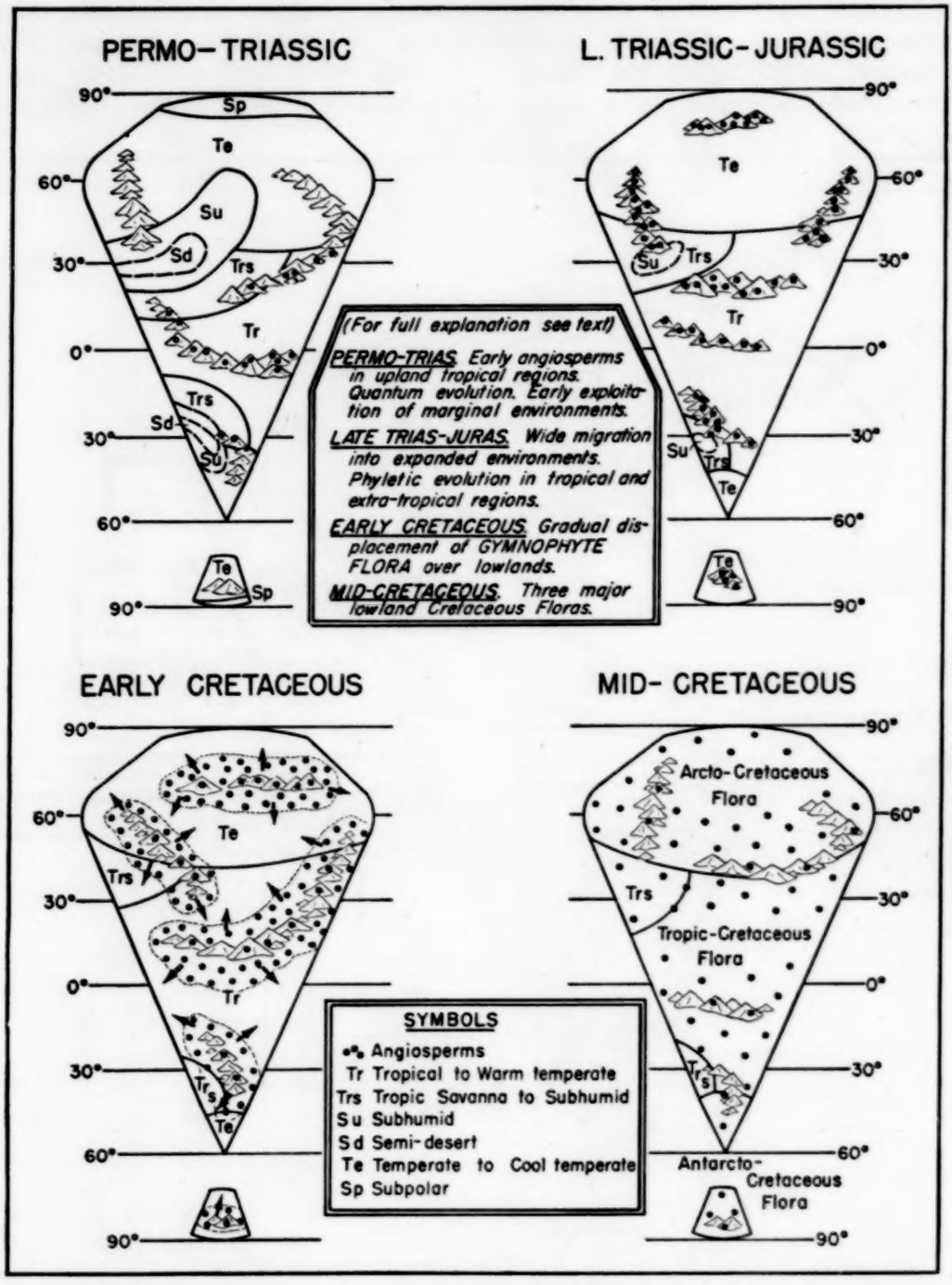

FIG. 11. Hypothetical stages in evolution of angiosperms following initial appearance of phylum in Permo-Triassic upland tropical regions.

the preceding or succeeding periods, diverse, drier subclimates must have existed over the tropical region, much as they do at present. Such environmental diversity would be particularly important to early angiosperm evolution at this time for it would tend to promote the origin of new adaptive types in the initial angiosperm populations. In brief, conditions then would have been most propitious for quantum evolution (Simpson, 1944, pp. 123–124; Stebbins, 1950, pp. 508–510).

The present hypothesis is that early angiosperms were in a quantum phase, differentiating from proangiosperms of still unknown character and ancestry.

Conceivably they could have evolved from an ancient seed fern stock which was confined primarily to upland regions throughout its history and is still unknown in the fossil record. In any event, the basic type is visualized to have undergone ecological fragmentation, and evolution was progressing eruptively. The probable nature of the early evolution of basic angiosperm types, as discussed recently by Stebbins (1950, pp. 508–510), supports the belief that many basic types may have appeared in a relatively short time in the diverse upland environments. Simpson (1944, p. 212) has noted that populations in the transitional phase of quantum evolution are scarcely qualified to meet strong competition from populations already occupying the zone. It is pertinent that during Permo-Triassic time much of the upland vegetation of gymnosperms and ferns (Gymnophyte Flora, fig. 12) was moving down into the lowlands to replace the older Pterophyte Flora (fig. 12) dominated by arborescent lycopods and arthrophytes and their associates, to become the dominant lowland vegetation. Thus with the opening of new sites in the uplands initial angiosperm populations in the quantum phase probably would have encountered relatively little competition.

Emphasis must be placed on the idea that these early angiosperm populations were differentiating not only in the humid tropics, but also in the diverse subtropical and marginal tropical environments which were then in existence. The inference is strong that most of the early evolution took place within the varied environments of a broader tropical zone than exists today, and that the derivatives of this group were confined largely to warmer regions of the world throughout their later history. For a number of early types, however, evolution may have been directed also into the margins of the cooler and drier environments situated both to the north and south of the tropical to warm temperate belt. In some families, on the other hand, early evolution may have taken place not only within the tropics, but also on the borders of extra-tropical environments lying largely in austral regions, whilst other groups at this early date may have commenced to exploit the tropics as well as the margins of extra-tropical environments situated in regions to northward. Thus by the later stages of the quantum phase some groups may have expanded well into the extra-tropical areas. On this basis certain types derived from basic tropical stocks that were preadapted to the drier and cooler regions marginal to the tropics may have appeared very early in angiosperm history. This might well account for the antiquity which must be postulated for a number of peculiar plant forms that are found today on the margins of the tropics, representing such families as Cactaceae, Didiereaceae, Euphorbiaceae (south African types), Apocynaceae (*Pachypodium*), and Fouquieraceae (*Idria*). Significantly, these peculiar plants largely belong to basically tropical families. Finally, we may suppose that not all lines in evolution were "successful," but that numerous "experimental" types were evolving, some of which lasted for longer or shorter periods of time, and that numerous intermediate or "linking" types were represented. Since all these plants were limited to upland regions, to sites remote from the lowland areas of sedimentation where most of the record was being assembled and preserved, we have no record of them.

Late Trias-Jurassic. There was world-wide moderation of climate during this interval (Seward, 1931; Chaney, 1948). We may infer that with the restriction and elimination of the more diverse and more extreme continental climates of the preceding stage, some of the earlier experimental and transitional types now became extinct as their more localized environments decreased in area and tended to disappear. Such extinction would tend to produce discontinuities between earlier, more closely related categories (species, genera, families), thus setting off in wholly random manner higher groups of

quite variable taxonomic magnitude within the surviving types.

The latter, which are considered to have been confined earlier to rather restricted Permo-Triassic upland environments within and adjacent to the tropics (fig. 11, Permo-Triassic), could now expand in upland areas, for climatic moderation had produced a broad tropical zone flanked at higher latitudes by temperate climates, with savanna conditions in existence at low-middle latitudes (fig. 11, L. Trias-Jurassic). Angiosperms probably tended to differentiate greatly in these larger areas in response to newly available habitats and subclimates. This supposition finds support in the evolutionary history of ferns, seed ferns, lycopods, coniferophytes and cycadophytes, all of which attained greatest diversity at times of maximum extent of the environments most suited to them. Thus we may infer that evolution of the phyletic type, as visualized by Simpson (1944, pp. 202–206), now proceeded in many family groups. Those in tropical to warm temperate regions, and most family types are thought to have been concentrated there, now diversified within this wider climatic zone. Those tropical families which had earlier commenced to exploit the marginal extra-tropical environments to which they were preadapted probably spread more widely, invading the temperate to subhumid regions both to the north and south. Other tropical families may have exploited cooler and drier environments lying chiefly in austral extra-tropical areas. Some could have continued to differentiate not only within the tropics, but also in northern extra-tropical environments as well. Thus the fundamental patterns in distribution that are clearly apparent in our day may easily have had their origins at this early date. This does not mean that families lying largely in austral regions today may not have ranged into the northern latitudes. Some of them, such as the Proteaceae and Myrtaceae, certainly have had such a distribution to judge from the Cretaceous and Early Tertiary floras. Nonetheless, it must be emphasized that they were chiefly within the wider tropical to warm temperate belt at that time. The inference is strong that these and other families have had their chief center of evolution and distribution in the tropical and austral regions during most of their history.

Thus by the end of the Jurassic many angiosperm families probably had developed in upland areas. They were now differentiated into major vegetation types defined primarily by climate, tropical through the broad central region, flanked by temperate types at higher latitudes, with subhumid communities at low to middle latitudes in the western portions of the land areas. In each of these regional vegetation areas numerous adaptive types were now represented in the different families. These ranged from trees and shrubs to lianes and herbs in many alliances, while the more primitive groups largely maintained their more primitive tree-like character. Although the pattern of family occurrence at this time was primarily one of tropical distribution, some now ranged into extratropical regions both to the north and south, while others were distributed from the tropics largely into austral, or into northern extratropical environments. Aside from a few records of pollen, wood and leaves which entered the lowland Jurassic sediments (fig. 1), we have little information on these plants which were still evolving in the more distant upland regions.

Early Cretaceous. Angiosperms gradually invaded lowland areas during the Early Cretaceous, and displaced slowly the gymnosperm-fern flora which had been dominating the lowland regions since the Late Permian. Displacement of this older Gymnophyte Flora probably was easy, at least in the sense that angiosperms were now better adapted to the lowland environments throughout the world. They had a more rapid and efficient means of reproduction, and also had the advantage of bird and insect pollination. Further-

more, sites suitable for occupancy were now to be found everywhere in the lowlands, for ecologic competition was relatively low. Thus, when they first appeared in the record in appreciable numbers, angiosperms were already highly developed, with categories of order, family and generic rank well outlined. In addition to many modern families and genera, these floras also contain ancient types which were largely eliminated by the end of the period. Forms such as *Credneria, Protophyllum* and others may belong to this group.

The transformation in the plant world during the Cretaceous, involving the replacement of the Gymnophyte Flora by the Angiophyte Flora (fig. 12, right column), brings us face to face with one of the problems in angiosperm evolution which has been under discussion for over a century and a quarter. As mentioned earlier (page 29), Darwin referred to this so-called "sudden transformation" as "an abominable mystery." He was making reference here to a conclusion which had been reached some years earlier by Brongniart and contemporary paleobotanists. They had concluded from their studies of Cretaceous floras that angiosperms suddenly attained a position of dominance in the plant world during Cretaceous time, and that this rapid transformation was one of the most remarkable facts in evolution. The concept of the sudden appearance of angiosperms in the record was accepted without reservation by most investigators during succeeding decades, and is still generally considered as an established axiom of historical geology. The following statement, for example, will serve to show how one author has recently expressed the problem (*also see*, Seward, 1931, p. 520; Darrah, 1939, p. 342; Walton, 1940, p. 165; Just, 1948, p. 97; Whitehouse, 1950, p. 199).

"One of the most remarkable phenomena in biological evolutionary history is the rapidity with which the angiosperms arose to a position of dominance in the plant world during the latter part of the Mesozoic era" (Arnold, 1947, p. 333).

This current belief in a sudden transformation from one kind of vegetation to another has an undeniable flavor of the catastrophism which still pervaded some investigations of the natural world during the early half of the last century at which time the concept had its inception. As far as can be determined, there is not one shred of evidence to support the assertion that angiosperms suddenly arose to dominance. Perpetuation of this idea for over a century apparently rests on two fundamental misconceptions. In the first place, its adherents seem to have had no real appreciation of the fact that the lengths of time represented by the geological periods are in no wise equal. If we plot geological time according to scale in terms of millions of years, as shown in figure 12, it becomes apparent that the angiosperm flora assumed dominance no more rapidly than the other great land floras which preceded it. Prior to the lowland history of angiosperms, three major World Floras occupied lowland regions where their remains entered the sedimentary record (fig. 12). These included (1) the Psilophyte Flora, dominated by psilophytes, and by primitive lycopods, arthrophytes and ferns, ranging from the Late Silurian to the end of the Devonian, (2) the Pterophyte Flora, characterized chiefly by dendroid lycopods and arthrophytes, and by ancient ferns, seed ferns and primitive conifers, ranging from the end of the Devonian into the Permian, and (3) the Gymnophyte Flora, exemplified by coniferophytes, cycadophytes and ferns, ranging from the Permian into the Early Cretaceous. The successive changes between these Floras were gradual, taking place during some 20 million years, in which time older types were replaced gradually by newer. It is apparent that angiosperms gradually displaced the Gymnophyte Flora during an interval of generally similar magnitude.

The second source of error made by adherents of the theory of the sudden rise of angiosperms to dominance seems to lie in the tacit assumption that there has

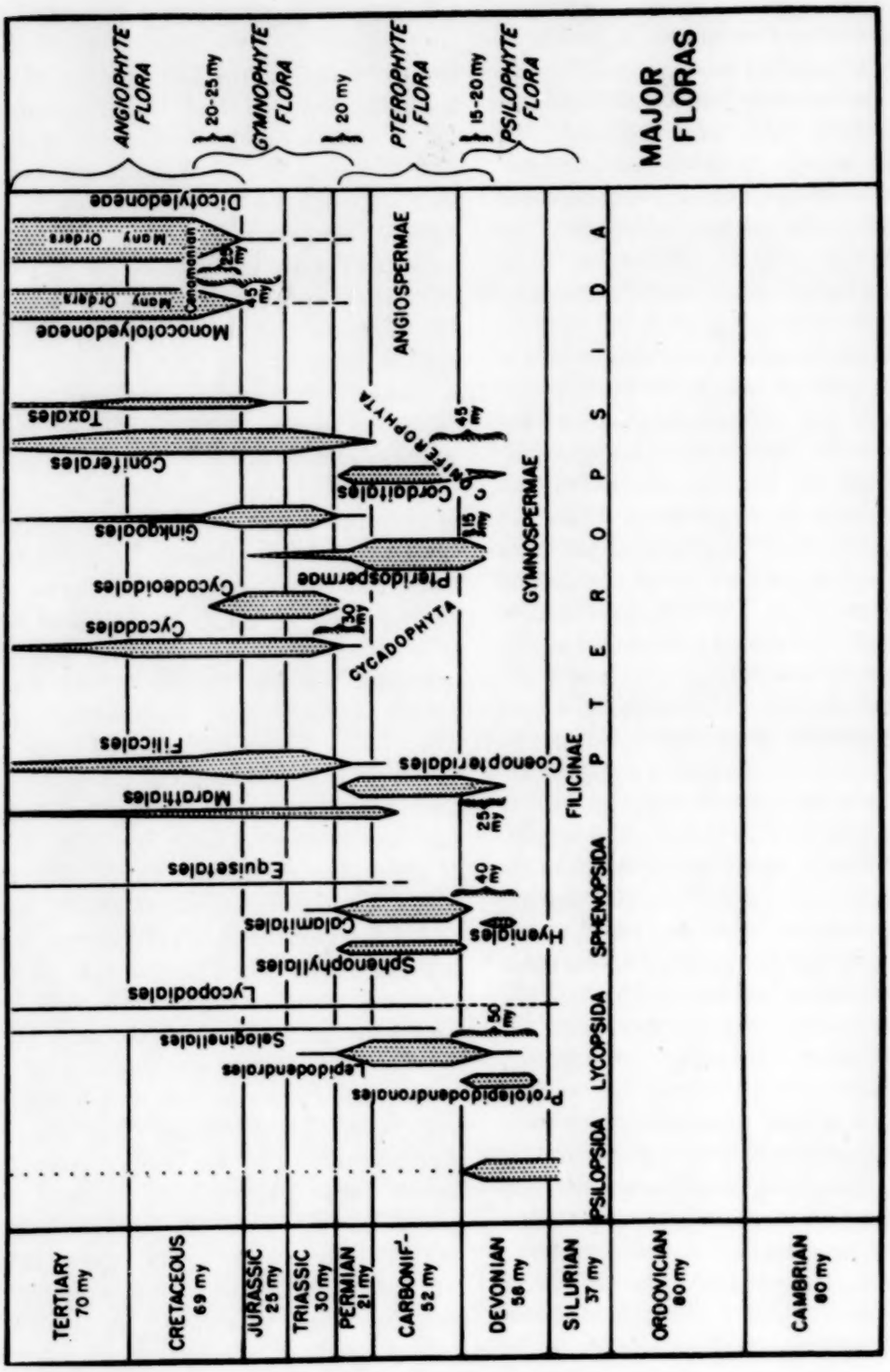

FIG. 12. Showing approximate time (in millions of years) for (*a*) replacement of World Floras (right column), and for (*b*) phyla of vascular plants to rise to dominance following first appearance in record.

been a sort of standard time rate in the rise to dominance by the major plant phyla, and that angiosperms have greatly exceeded this rate. Such a supposition finds no support in the known history of the major plant groups. Figure 1 shows some of the records of Mesozoic angiosperms which can be used for comparison with other groups of vascular plants. We may use the Early Cretaceous angiosperms, which gives us an interval of some 20 to 30 million years from time of first appearance to Cenomanian dominance. We can use the few Jurassic records (and this is a more proper datum), which will then make the interval from first appearance to dominance on the order of 40 to 50 million years. The probable angiosperms of the Triassic would represent an interval of some 60 million years from first appearance to dominance in the Cenomanian.

Regardless of the datum we select for comparison, it is possible to demonstrate that angiosperms paralleled other groups in time required for rise to dominance, that some groups have developed more slowly, that others have been more rapid. Referring to figure 12, we find that within the range of 20 to 30 million years suggested by Cretaceous angiosperms that seed ferns exceeded angiosperms in rise to dominance, that cycadophytes and ferns paralleled angiosperms, and that arborescent lycopods, arthrophytes and coniferophytes developed more slowly. Using the 40 to 50 million year interval suggested by Jurassic angiosperms, we see that angiosperms are exceeded in rise to dominance by seed ferns, cycadophytes and ferns; they are paralleled generally by arthrophytes, lycopods and gymnosperms. Should we use the Triassic records as a datum, then the angiosperm phylum would have taken a longer time to rise to dominance than any other group. Thus comparative evidence on time required for other phyla to rise to dominance following their initial appearance in the record shows also that angiosperms gradually assumed a position of dominance in the plant world during the middle and later Mesozoic. From these data it is apparent that angiosperms must be removed from the category of "miracle plants."

4. *Middle Cretaceous.* From an analysis of the first lowland Cretaceous floras which contain angiosperms in abundance, notably those of the Cenomanian and succeeding stages, it is evident that three regional floras had become differentiated (Axelrod, unpubl. data). A tropical to warm temperate flora characterized the lower and middle latitudes in the warmer and moister parts of the world. Although there were differences from east to west, and from north to south, we do not have sufficient data to determine whether they were of a magnitude comparable to those which had developed by the Early Tertiary.[6] The temperate floras at higher northern and southern latitudes, however, differed greatly from one another early in the period (Berry, 1937). For these earliest lowland angiosperm floras the terms Tropic-Cretaceous Flora, Arcto-Cretaceous Flora, and Antarcto-Cretaceous Flora seem generally suitable.

There are clear indications in all Cretaceous (and Eocene) floras that particular types were in general more widespread and comingled and were less segregated than today. Some Cretaceous angiosperms apparently included a greater diversity of species within genera than these same genera have today. Cain (1944, p. 75) has pointed out that breadfruit (*Artocarpus*) which is now strictly tropical, and which has been recorded at higher latitudes, may have been represented in Cretaceous and Early Tertiary floras by one or more temperate to warm temperate species, as in the case of certain genera today, such as persimmon (*Diospyros*), avocado (*Persea*) and magnolia (*Magnolia*). We may add in this connection that a number of genera which are

[6] Paleoclimatic evidence suggests that the Paleocene to Early Eocene floras may have been more nearly pantropic in character than those of Cretaceous age.

frequently regarded as temperate, such as alder (*Alnus*), maple (*Acer*), birch (*Betula*), haw (*Crataegus*), katsura (*Cercidiphyllum*), sweet gum (*Liquidambar*) and sycamore (*Platanus*), were widely represented in the warm temperate to subtropical zone during the Cretaceous and Early Tertiary. Pertinently, many of the widely distributed families in the northern hemisphere which are often considered as temperate, including the Aceraceae, Betulaceae, Fagaceae, Rosaceae, Ulmaceae and others, extend into the tropics. The most primitive living species of maple, poplar, birch, oak, cherry and hackberry are largely evergreen types, and are found in warm temperate to tropical regions. Furthermore, these groups have either been derived from tropical families, or else their more primitive tribes and genera are in tropical regions today (Camp, 1947, p. 177; Croizat, 1947, pp. 63–65). By recognizing that some present day tropical and temperate genera probably included species during the Cretaceous and Early Tertiary that were adapted to both temperate and tropical environments, respectively, we may more readily understand how genera of present tropical distribution were able to mingle with those which are now almost wholly temperate in character. The few warm temperate to temperate species representing present day tropical genera, and the occasional warm temperate to subtropical species representing temperate genera, have become extinct since the Early Tertiary. As a result, the modern genera are represented by species which are no longer associated in living floras.

The earliest angiosperm floras represented by abundant material provide clear evidence of the distinctiveness of the floras in the northern and southern temperate regions, both of which appear to contain families that are not known now from the other area (Axelrod, unpubl. data). These are the families that presumably differentiated from the tropics into the northern and southern extratropical areas during most of their earlier history. These floras show also that many families are represented largely within the confines of the Cretaceous tropical world. These are the groups that are clearly and preponderantly tropical and apparently have always had their greatest diversity there. On the other hand some of the typically tropical families are found to extend into both the northern and southern extratropical regions. Some of the families which are now restricted to subhumid areas at lower latitudes in the western portions of the continents probably were also in existence at this time. Figure 13 shows in pictorial manner certain inferences which can reasonably be made with respect to the general relationships of Cretaceous angiosperm families. The size of the blocks represents the proportion of angiosperm families in each distribution pattern: tropical, tropical and extratropical, tropical and south, tropical and north, and extratropical in the cooler and drier regions. The arrows, which suggest the probable derivation of families in these patterns during geologic time, strongly indicate that the bulk of basic angiosperm types seem ultimately traceable to a source in the ancient tropics.

The data seem to support the view that angiosperms have not had an exclusively holarctic source, or a wholly austral center of origin. They were being assembled in both regions by the gradual adaptation of basic tropical groups to extratropical conditions during the long period from the Permo-Triassic down to the Cretaceous. On this basis, the Arcto-Cretaceous and the Antarcto-Cretaceous Floras of higher temperate latitudes represent vegetation types whose genera were derived largely by the long and continued differentiation of successively derivative members of originally tropical and border-tropical angiosperms. The basic stocks were slowly and gradually deploying into extratropical environments in highland regions from the Permo-Triassic to the Middle Cretaceous, an interval representing fully 90 million years in earth history. From

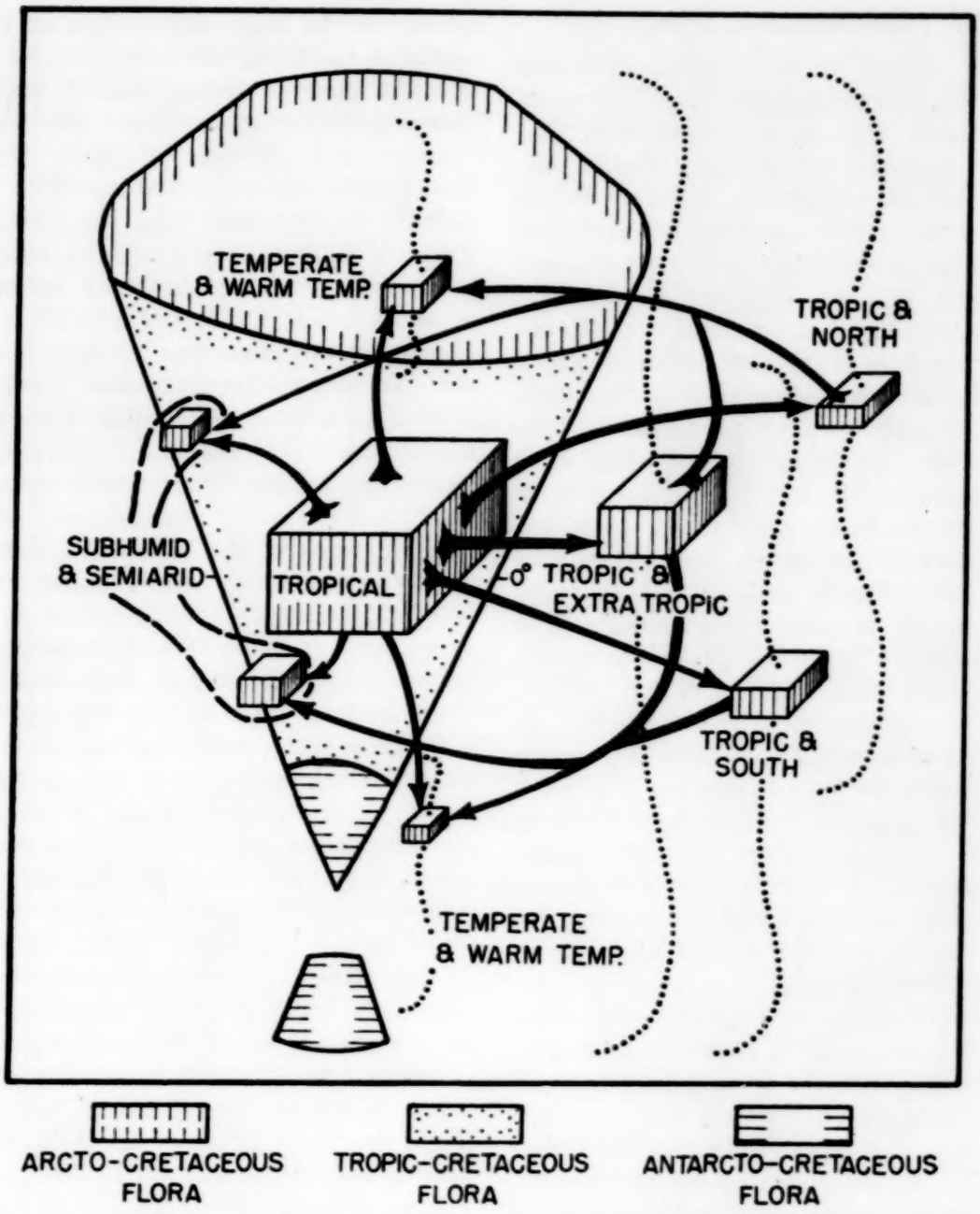

FIG. 13. Presumed basic family distribution patterns in Cretaceous time. Size of blocks suggests relative numbers of family types in each pattern. Arrows suggest probable derivation of families in each pattern.

this standpoint, the temperate regions to the north (holarctic) and south (antarctic) are subordinate or secondary centers in early angiosperm evolution, as are the drier areas marginal to them. Thus while the northern and southern temperate latitudes of holarctica and antarctica have been the source of the Arcto-Cretaceous and Antarcto-Cretaceous Floras, and also of their lineal descendants, the Arcto-Tertiary and Antarcto-Tertiary Floras, these areas have not been the centers of all angiosperm evolution. They are derived or secondary centers in angiosperm evolution. They have, nonetheless, shared equally with the tropical zone as the principal centers of radiation (migration) for angiosperm floras during the past 100 million years in which such floras have dominated lowland regions.

Post-Cretaceous Floras

The nature of angiosperm evolution since the Cretaceous has largely been of a different type as compared with that which characterized the first 90-odd million years in angiosperm history. While we are still concerned with the evolution of numerous species, of many genera, and of some families (largely herbaceous), the most conspicuous changes in the Cenozoic have been in the distribution of plants and in the composition of plant communities. Our attention now is focused chiefly on trends of climatic change which have been responsible for (1) major migrations of the basic, generalized vegetation types which had earlier been established over the lowlands, and for (2) changing composition of plant communities due to the selective influence of changing climate. The climatic trend of the Tertiary largely represented a shift toward increased continental environments, with a localization of humid and an expansion of drier climates. These modifications, which account in large part for present day patterns in distribution, have tended to disrupt and obscure the basic plan that had largely evolved in highland regions in pre-Cretaceous time. The broad outlines of Tertiary and Quaternary evolution are summarized below in four principal steps and are shown diagrammatically in figure 14.

Early Tertiary (Paleocene-E. Oligocene). At the outset of the period moderation of climate permitted expansion of the Tropical-Tertiary Flora to latitudes 55° N and 45° S, thus confining the Arcto-Tertiary and Antarcto-Tertiary Floras to higher latitudes (Chaney, 1948). This had an important two-fold effect. Further evolution of warm temperate to tropical species took place in the expanded Early Tertiary environment, particularly the modernization of species as well as the development of new species in the newly available environments of this wider tropical zone. At higher latitudes many near-modern forest species came into existence, possibly as a response to the long photoperiod at these latitudes. During the later part of this stage a general trend toward lowered temperature commenced, and the Arcto-Tertiary and Antarcto-Tertiary Floras now slowly shifted toward middle latitudes. At the same time the Tropical-Tertiary Floras were gradually confined to more coastal and to more southerly areas (Chaney, 1936, 1947, 1948).

Further evolution was initiated in both the Temperate-Tertiary and Tropical-Tertiary Floras by the middle of the stage as subhumid climates gradually appeared and expanded over lower middle latitudes. Important evolution was underway on the drier margins of the Temperate-Tertiary Floras in subhumid temperate regions, in which deciduous shrubland and prairie types now evolved. On the margins of the mesic tropical region, numerous types developed in drier border-tropical environments. This evolution has been particularly important, and has continued down through the Tertiary, resulting in the successive appearance of subtropical savanna and dry subtropical forest (Eo-Oligocene), arid subtropical scrub (Oligo-Miocene), woodland and chaparral (Oligo-Miocene), plains grassland (Pliocene) and warm desert (Latest Cenozoic) as regional types of lowland vegetation.

Many Late Cretaceous and Early Tertiary pantropic genera were eliminated from the New or from the Old World during this stage, tending to differentiate further the tropical floras. With the development of drier climates at lower latitudes across Eurasia during the Late Eocene, discontinuities developed in the Paleotropical-Tertiary Flora, differentiating it gradually into a western (African) and an eastern (Australasian-Polynesian) sector. Often sight is lost of the fact that there are far more genera common to the tropical regions than to the much larger land area of temperate holarctica (250 vs. 160 genera), and that types having discontinuous distributions across the tropical regions are more numerous than are those across the temperate areas (460 vs.

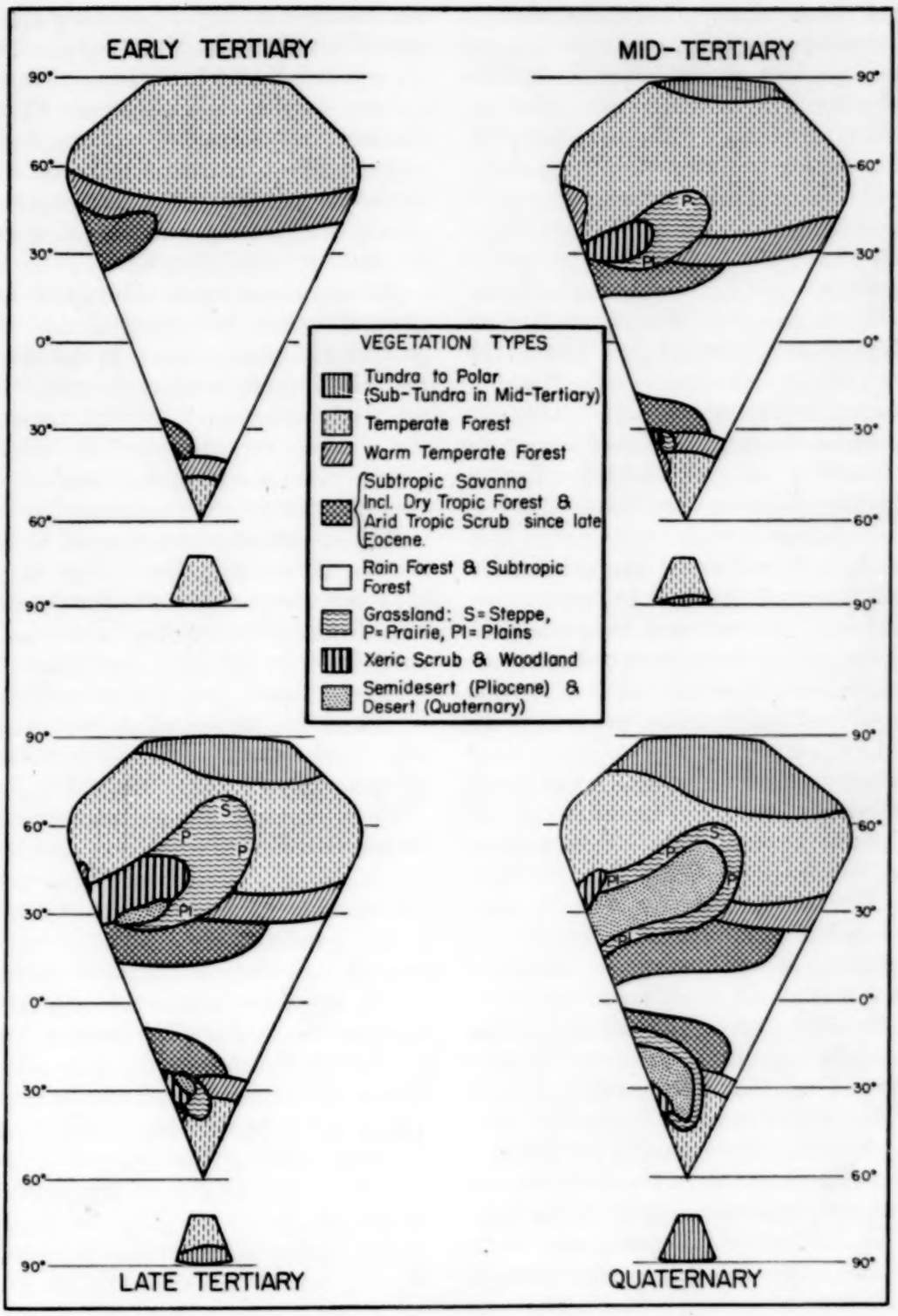

FIG. 14. Stages in Cenozoic evolution of modern vegetation.

127 genera). The long generic lists compiled by Good (1927; 1947) clearly demonstrate a distribution pattern across the tropics similar to that of the temperate segregates of the Arcto-Tertiary Flora, with pantropic, discontinuous and endemic types analagous to those at the north. These distributional relations clearly indicate the nature of the earlier affinities across the wider tropical belt of the Early Tertiary and Late Cretaceous, relationships which were largely disrupted by

the end of the Early Oligocene, though on all continents a few relic tropical types lingered on into the Pliocene in milder coastal sites at more temperate latitudes.

Middle Tertiary (M. Oligocene-M. Miocene). By this stage the Temperate-Tertiary Floras had shifted to middle latitudes from their Early Tertiary high-latitude lowland distribution. Lower temperatures at high latitudes, and the diversification of dry climates at low to middle latitudes, tended to disrupt the former transcontinental Arcto-Tertiary and Antarcto-Tertiary Floras. This climatic trend toward increased diversity and intensity of continental climates started the climatic selection and segregation of formerly more widespread species, and finally restricted them to regions situated largely latitudinal to one another (see below). Evolution of temperate forest herbs and grasses, especially in the prairie regions, now increased as forests retreated and open areas gradually expanded.

Further contraction of the humid Tropical-Tertiary Floras is recorded as the dry regions expanded during this stage, and as temperatures generally were lowered. Differentiation of species in marginal tropical environments (dry forest, arid subtropical scrub, savanna) increased as these subhumid areas expanded.

By the Oligocene, autochthonous semiarid continental floras, like the Madro-Tertiary Flora in southwestern North America, had gradually appeared over lowlands in the developing dry regions at lower middle latitudes. Their species and genera were derived chiefly from the Tertiary Floras which had previously occupied those areas, from the Arcto-Tertiary and Neotropical-Tertiary Floras in North America (i.e., the Madro-Tertiary Flora); from the Neotropical-Tertiary and Antarcto-Tertiary Floras in South America; and from the Arcto-Tertiary and Paleotropical-Tertiary Floras in Eurasia and North Africa. In all cases the plants represent further adaptation to drier environments. Judging from my studies of the Madro-Tertiary Flora, they appear to have evolved earlier in upland sites, chiefly on leeward slopes, in these same latitudes.

Late Tertiary (U. Miocene-Pliocene). During this stage a near approach to present day continental climates resulted from the expansion of dry interior regions, and the appearance of sub-polar climates at high latitudes.

As new, open environments of subcontinental extent became available for exploitation, grasses and herbs formerly confined to communities marginal to forest and woodland invaded these open areas and evolved rapidly (Axelrod, 1948). Evolution in the border-tropical communities (scrub and forest) continued as dry environments increased in area at lower middle latitudes. This may well have been responsible also for the production from wider-ranging types of some paired-species in the arid subtropical scrub, savanna, and plains communities marginal to the tropical regions north and south of the contracting rain forest environment (Axelrod, 1950).

Final disruption of transcontinental Temperate-Tertiary Floras was completed during this stage. Temperate forest species were confined gradually to more restricted regions which are now largely latitudinal in relation to one another, as between eastern North America, western North America, eastern Asia and Europe in the case of the Arcto-Tertiary Flora, or between the Tasman and Fuegian regions in the case of the Antarcto-Tertiary Flora. These present day forests are relics of earlier transcontinental temperate Tertiary Floras of more generalized composition which have survived in regions of more restricted environments.

Quaternary. Great differentiation of new types has taken place chiefly in herbs and grasses in the newly expanded Late Cenozoic environments (tundra, desert) which resulted from the continued trend toward increased continental conditions and the consequent restriction of forest, woodland, and scrub vegetation. At the

same time, due in large part to intense mountain building during the Late Cenozoic, numerous micro-environments developed in most regions. Many woody and herbaceous plants exploited these more restricted areas by the production of innumerable ecologic types, especially by polyploidy.

The summer dry regions of Mediterranean climate (central and southern California, central Chile, Mediterranean basin, southwest Australia, South African Cape region) also have been important areas of recent evolution, particularly for herbaceous and shrubby species. These plants represent derivatives of genetically variable populations whose ancestors were present in those regions in the Late Pliocene. They spread widely and adapted rapidly to the diverse environments of these subhumid regions as species requiring summer rain disappeared at the end of the Pliocene, and new environments became available for exploitation.

Another important change which has resulted from the appearance of present-day climates during the past million years has been the development in all vegetation types of numerous, more localized communities adapted to narrower environments; these are communities derived from the earlier, more widespread and more generalized Tertiary Floras by the climatic selection of types suited to more restricted climatic regions.

Major migrations are recorded in meridional directions during this stage, largely in response to the fluctuations of Pleistocene climates. Invasion of high mountains in the tropics by cool temperate boreal herbs is recorded, and some probably were involved in trans-tropic migration as well (Axelrod, 1950).

Summary

The following theory of angiosperm evolution may explain the history of the phylum following its initial appearance from a still undiscovered proangiosperm stock (or stocks).

Permo-Triassic. Geological and botanical data are adduced which support strongly the inferences that (1) angiosperms probably were in existence by Permo-Triassic time, that (2) they probably occupied upland regions remote from lowland sites of deposition, that (3) they were distributed in the diverse environments of the tropical zone, that (4) at least some of them were ancestral to modern primitive types of monocotyledons and dicotyledons which are now represented in tropical regions, and that (5) they were then undergoing quantum evolution from proangiosperms which occupied upland regions.

While most groups were confined initially to the tropical zone, during the quantum phase some family types probably started to exploit the more extreme marginal environments of the uplands which were prominently developed during this stage. Some tended to differentiate from the tropics both north and south, others evolved within the tropics as well as in marginal environments to southward, whilst some probably exploited the tropics as well as adjacent regions lying to northward. None of these early types has yet been recorded.

Late Triassic-Jurassic. With a return to more equable climates during this stage, some of the types which had developed earlier in the uplands of the more extreme tropical and marginal tropical environments probably became extinct as their areas tended to disappear. This created in random manner numerous discontinuities between the earlier more closely related groups. Expansion of humid environments now enabled surviving types in upland areas to exploit the broad regional climates, and most groups probably were now evolving in the mode of phyletic evolution. Although many angiosperm families probably had developed in the uplands, only a few have been recorded in lowland deposits of this age. Nonetheless, both monocotyledons and dicotyledons of present day primitive family types appear to be recognizable.

Early Cretaceous. Angiosperms attained some diversity of type over the lowlands during the Early Cretaceous, and by the middle of the period had displaced the older Gymnophyte Flora over the lowlands. Replacement was gradual, not with "bewildering suddenness," as judged from comparative data representing (a) time required for other major World Floras to rise to dominance, and (b) the time required for other phyla to assume dominance.

Three major Cretaceous Floras (Arcto-Cretaceous, Tropic-Cretaceous, Antarcto-Cretaceous Floras) were assembled over the lowlands by migration from adjacent uplands where they had been evolving during the Jurassic and earlier. That the area of basic angiosperm evolution was the tropical zone is indicated by the fact that the phylum is adapted primarily to tropical environments, and secondarily to the more specialized tropical and extratropical regions. The pattern of distribution shown by both fossil and living floras, of typically tropical families, tropical groups exploiting either boreal or austral regions, and the presence of derivative families in extratropical regions, reflects a trend in evolution which probably started early in their history. All known evidence therefore seems to indicate that the temperate holarctic and antarctic regions, as well as the drier areas, are secondary centers in angiosperm evolution.

By the dawn of the Cenozoic many essentially modern species had evolved from their near-modern ancestors. This tended to differentiate the Arcto-Tertiary, Antarcto-Tertiary, Paleotropical-Tertiary, and Neotropical-Tertiary Floras from their Cretaceous counterparts.

Cenozoic. Three principal migrations are recorded over the lowlands during the Tertiary. With the moderation of climate early in the period, Tropical-Tertiary Floras extended to latitudes 55° early in the stage, confining the temperate Floras to higher latitudes. In response to the lowering of temperature during and following the later Eocene, the Temperate-Tertiary Floras shifted to middle latitudes by the Oligo-Miocene, confining the Tropic-Tertiary Floras to coastal positions and to lower latitudes. The appearance of dry regions at low to middle latitudes following Early Eocene time permitted the expansion in radial manner of semiarid autochthonous Floras derived from the temperate and tropical Floras which had earlier occupied these areas. This trend toward aridity culminated with the appearance of subcontinental deserts at the end of the Cenozoic, although local subdesert areas had earlier been present. The gradual spread of drier and cooler climates during the Tertiary tended to restrict the Tropical- and Temperate-Tertiary Floras to more humid, and to warmer regions.

Climatic selection, with attendant geographic extinction, disrupted the primary Cretaceous to Eocene patterns of distribution and accounts for those of the present day. In the latitudinal pattern, earlier pantropic to subpantropic groups were largely disrupted by the end of the Eocene, to survive in regions of more localized tropical climate. Temperate forests formerly ranging across holarctica and antarctica were confined to more restricted areas during the Miocene and Pliocene, being replaced by steppe and subdesert regions. In meridional patterns across the tropics, discontinuities have been developing throughout the Tertiary: for tropical types early in the period, for subhumid and semiarid types later in the stage. Radial patterns in distribution across the present desert regions appeared largely during the later Cenozoic.

The Quaternary witnessed the development of hosts of ecologic forms from earlier wide-ranging types. These ecotypes have enabled species to adapt to still more restricted environments which result from continued mountain building and further localization of environments. Major migrations are recorded in response to the advances and retreats of

ice sheets, and the fluctuation of pluvial stages at lower latitudes.

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THE ECOSPECIES—PRELUDE TO DISCUSSION

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Introduction

Ever since Darwin wrote "The Origin of Species," it has been customary for many biologists to talk of evolution and speciation almost as if the two terms were completely interchangeable and, as a result of this implication, to consider the species as a unit of evolution. Thoday (1951) has sounded a very necessary warning that this usage is incompatible with the use of the same term to represent a classificatory unit. Depending upon the breeding system, the unit of evolution may be less than the species, equal to it or contain several species. Furthermore, a sudden change in either external or internal conditions may produce a considerable change in the size and complexity of the unit of evolution. This applies no matter how many aspects of biology are taken into account in framing the species-concept.

The boundaries and significance of the taxonomic species vary enormously according to the particular group of organisms in which it is sought and according to the amount of critical attention which has been given to that group. There is no single definition of a species which is applicable to all situations. The very fact that a large number of criteria are involved and that some of them are subjective gives the species-concept a flexibility which is highly desirable for many purposes but seriously diminishes its usefulness in making comparisons between groups.

Gilmour and Turrill (1941) have shown that while such a "general" classification must be maintained, there is value in experimentation with "special" classifications (based upon a limited number of kinds of attribute) for special purposes (see also Turrill, 1938*a*, *b*; 1946). "Biosystematics" (or "Experimental Taxonomy"), compounded from Turesson's originally ecological system and Danser's "fertility-sterility" system, represents such a special classification and its value is in the analysis of problems of the genetics of wild populations. Whether or not it is well named is beside the present point. Because of its simple ecological and genetical basis, biosystematics is restricted in its range of categories, the comparium representing the uppermost limit. For just this reason, its applicability to evolutionary problems is confined to what has been called "micro-evolution." In this case, wherever the possibility and extent of gene-exchange is important, the biosystematic units show their usefulness. They have much less significance than orthodox taxonomic categories in indicating phylogeny, because "individuals with a large number of attributes in common owe their resemblances usually and broadly speaking to closeness of parent-descendant relationship" but their "similarity is not necessarily an *exact* measure of their relationship" (Gilmour and Turrill, 1941). When the classification is based upon a few attributes or even only one, the measure must be even more approximate.

At present, however, our special classification is imperfect and a part of the imperfection is the lack of agreement between different groups of workers as to the exact criteria involved. There seems no reason why discussion of the problems should not remove these differences for they are not fundamental. Most authors emphasize the importance of restrictions upon gene-exchange when plants are grown in an experimental garden although others would judge from the sit-

uation in nature (and show a tendency to try to make the ecospecies exactly equivalent to the taxonomic species).

Definition of an Ecospecies

Criteria involved

Gregor (1944) and Turrill (1946) have pointed out that there have been several modifications of the terms *ecotype, ecospecies,* and *coenospecies* since they were first introduced by Turesson (1922). In part, this modification has been the result of increasing precision on the part of the pioneer author himself (cf. Turesson, 1929) but further definitions have been added by subsequent authors and these are reprinted in Appendix 1. Most recently, significantly different definitions of ecospecies have been proposed and defended (Valentine, 1948, 1949) (also see Appendix 1). The earlier of these states that "Species are ecospecies of a coenospecies when exchange of genes can take place between them but when the exchange under either natural or artificial conditions is limited in some way" (Valentine, 1948, p. 128). A similar reference to the limitation of gene-exchange under *either natural or artificial conditions* is contained in the later definition of "*g*-ecospecies" (Valentine, 1949). By this means forms which can produce fully fertile and strong hybrids after artificial crossing are allowed to qualify as separate ecospecies if they do not exchange genes freely in nature. The definition by Gregor, Davey, and Lang (1936) allows of much the same interpretation. Valentine (1949, p. 77) has been able to point to Turesson's (1929) definition in support of this (although Gregor (1944) has shown that, despite his definition, Turesson has been willing to accept *potential* full ability to exchange genes as a measure of inclusion within one ecospecies, even if natural gene-exchange is limited).

Thus, these definitions run counter to the generally held concept of isolation between ecotypes as purely ecological while that between ecospecies is partly ecological and partly "genetic." If they were to be accepted without modification, it would not be possible to draw a dividing line between ecospecies and ecotypes, for even ecotypes are prevented from the *free* exchange of genes in nature by their adaptation to separate environments. Another difficulty in the way of a definition of ecospecies upon their behavior in nature is that, in certain cases, gene-exchange between forms may be considerable in some localities while negligible in others. In some of the cases described in recent literature where hybrid swarms have formed as a result of local human modification of the environment (and this may be a common cause, cf. Heiser, 1949) we should have a situation in which, over the majority of their ranges, a pair of interfertile forms might pose successfully as ecospecies while in the modified area, only, would they demonstrate mere ecotypic distinction. Even then it might be difficult to be sure whether or not they were exchanging genes completely without limitation.

There are further innovations in the definitions proposed by Valentine and these are well worthy of discussion. In the definition of "*g*-ecospecies," "well-defined morphological, ecological and geographical differences" are called for between ecospecies (Valentine, 1949, p. 82) and, presumably, the failure to show any one of these differences will rule out ecospecific distinction between the groups involved. Apart from the debatable question as to what constitutes a "well-defined difference," are these specifications necessary? It is to be noted that for "*a*-ecospecies" the clear morphological distinction is not insisted upon because it very often will not exist. There seems no need to insist upon it in *g*-ecospecies merely because it will more often be there and, in any case, it is out of place in a ecologic-genetic "special classification." Clausen, Keck, and Hiesey (1939, 1940) have recognized that ecotypes and ecospecies may not be distinguishable mor-

phologically (and therefore not separately classifiable in orthodox taxonomy) but this has not prevented their recognition.

On the other hand, Valentine's definitions are the first in recent years to include positively the necessity for a pair of ecospecies to differ in ecological preference. Even in the definition proposed by Gregor, Davey, and Lang (1936), where differences in ecology are mentioned, they are not insisted upon as criteria for the separation of ecospecies. Such an insistence appears reasonable and preserves some of the original sense of the ecospecies.

If there are ecological differences between ecospecies, certain geographical differences are bound to follow. On the other hand, those geographical differences which have no connection with ecology (i.e., disjunctions of range involving similar climatic, edaphic and biotic conditions and due to purely historical factors) are outside the terms of reference of a cytogenetic-ecological classification and merely emphasize that there is no necessity for the inclusion of geographical differences in a definition of ecospecies.

The distinction between "*g*-ecospecies" and "*a*-ecospecies" is a worthy one and will certainly reduce the excessive heterogeneity which is shown by the ecospecies of orthodox definition. Although these new definitions carry the implication that the only kind of abrupt speciation is that which involves a change in chromosome-number, the exceptions (particularly in the genus *Oenothera*) are probably insufficient in number to cause acute embarrassment. The distinction of "*g*"- and "*a*-ecospecies" is, of course, only relative and a species which is a "*g*-ecospecies" in relation to a second species may well be an "*a*-ecospecies" in relation to a third.

Groups which are separated by genetic barriers but show no distinctions of morphology or ecology (or geography) are covered in Valentine's classification as cytotypes (and kept within a single ecospecies) provided that they are members of a polyploid series. It is perhaps unfortunate that there is no comparable category to contain groups equally well separated genetically but which have remained on the same chromosome-level. In both cases these groups are likely to represent incipient ecospecies and to be restricted in number.

Ecospecies and taxonomic species

The case of *Silene cucubalus* Wibel and *S. maritima* (Hornem.) With. is discussed by Turrill (1946) and Valentine (1948, 1949) as one example where the opinion of most biosystematists (regarding these forms as ecotypes of one ecospecies) is at variance with the opinion of most taxonomists (who would consider them to be satisfactorily distinct species). In fact these authors have defended admirably the case for regarding these campions as separate species in taxonomy but there is really no cause for us to alter our definitions of ecospecies to accommodate these exceptions to complete equivalence between taxonomic species and ecospecies. Similarly, attempts to narrow the concept of the species in orthodox taxonomy by putting this on a much more strictly genetic basis (notably those made by the zoologists Dobzhansky, 1937, and Mayr, 1942) need to be considered carefully before adoption by botanical taxonomists, particularly as they appear to be framed without the possibility of reticulate evolution in mind.

Where the biosystematist is also a practical taxonomist engaged in floristic work he has the right to use two forms of exposition, each to its own audience. Thus there is no inconsistency between the claim by Clausen (1949) that he and his associates "advocate a *coordination* of the information on comparative morphology (in which they include the number and morphology of the chromosomes), ecology, genetic and physiologic incompatibility, and chromosome homology as a key to better founded conclusions on taxonomic and evolutionary relationtions," and their simple genetical definition of an *eco*species.

Development of reproductive isolation

It is possible, at this stage, to consider also whether the genetical criteria by which ecospecific distinctions are decided upon are fully satisfactory. It would be unfortunate if the consequences of unnatural operations, such as the artificial pollination of flowers, should provide the only evidence for drawing conclusions about what is supposed to be a "natural" form of isolation between plants (cf. also Stebbins, 1945). This is especially the case when there is good reason for believing that it is in the differential attraction of insect pollen-vectors that some sympatric forms preserve their essential identities. There appears to be no valid objection to differences in flower-structure, differences in phenology, the presence of certation-effects and of "plasmon-sensitive genes," etc. (all of which may interfere with the free production of hybrids between forms) being included in the "genetic" isolation mechanisms which, if they are reasonably efficient, provide ecospecific separation.

Mather and Edwardes (1943) have pointed out that "if selective action has resulted in the origin of a bar to crossing, loss of relational balance between the isolated or partially isolated groups will occur and manifest itself as hybrid incapacity." Adaptation to distinct environments, such as is characteristic of separate ecotypes, constitutes the first bar to successful crossing in nature. Nevertheless, a decay of relational balance does not occur right away, otherwise the ecotypes (by definition) could exist only transitorily and would become ecospecies almost at once. This is especially true when the forms are geographically well-separated and there is no selection-pressure to favor the strengthening of bars to crossing (cf. Dobzhansky, 1937; Darlington, 1940; etc.).

This lag, necessary for the existence of ecotypes, must also be taken into account in the framing of a definition of ecospecies. Strengthening of the originally ecological bars to crossing may take place by mechanical or physiological means which have no effect upon hybrid capacity and there is no guarantee that even widely separated forms will not prove to be interfertile when the cross is made artificially. Thus, irregularity in rates of evolutionary divergence compared with the development of hybrid incapacity has been shown by Gajewski (1949) who found that fertile hybrids could be obtained by crossing species of *Geum* belonging to two different taxonomic sections while, on the other hand, those between *G. urbanum* and *G. aleppicum* Jacq. (which are morphologically much alike and belong to the same section) are quite sterile. In *Calochortus*, viable seed may be harvested from some intersectional crosses whereas species placed in the same subsection may be completely intersterile and a similar condition is demonstrable in *Balsamorhiza*. Ownbey and Weber (1943) suggest that this may be due to the development of the sections of the genera in geographical isolation from each other while the members of each section may evolve in closer contact.

Saunders and Stebbins (1938) have demonstrated that, in the genus *Paeonia*, the amount of meiotic abnormality in interspecific hybrids is not at all proportional to the difficulty with which the parents can be crossed, nor to the degree of taxonomic difference between them. In the peonies, isolation may be produced geographically, phenologically, by incompatibility in mating, by cytogenetic incompatibility resulting in asynapsis "or to a less extent by gross structural differences in the chromosomes." The pairing affinity of the chromosomes is of little or no value in deciding phylogenetic relationships. In a discussion of the origins of hybrid sterility in plants, Stebbins (1945) has shown that the several groups of species-isolating factors may develop independently to a great extent and certainly without correlation with morphological and ecological change.

In the animal kingdom, Moore (1949)

has shown that crossings between geographically separated races of *Rana pipiens* may produce less viable hybrids than those between this species and three other related species. Among plants this is to some extent paralleled by the progressive geographical variation in "plasmon-sensitivity" of genes in interracial crosses of *Epilobium hirsutum* L. (Michaelis, 1940, 1942; M. & von Dellingshausen, 1942) although highly fertile interspecific hybrids are not unknown in this genus.

An extreme example of a lag in the development of hybrid incapacity is to be seen in the formation of fertile hybrids × *Cupressocyparis Leylandii* (Jacks. and Dall.) between two species of the genera *Cupressus* and *Chamaecyparis* (Jackson and Dallimore, 1926). It is difficult to believe that they belong to the same ecospecies. Similarly, the genus *Aquilegia*, despite its wealth of ecological and morphological diversity and considerable geographical distribution shows remarkable interfertility between its constituent species (Clausen, Keck, and Hiesey, 1945). It is, therefore, of considerable interest that despite the ease with which artificial crossings may be made, an experiment by Anderson and Schafer (1933) showed that effective outcrossing of *Aquilegia vulgaris* with other species growing alongside it in a garden did not occur although at least 16% of outcrossing took place within the species. These authors believe this to be due to some intra-carpellary competition.

In view of these facts it seems that the development of hybrid incapacity occurs too irregularly to provide the only criterion of ecospecific distinction and to wait for it is, in a number of cases, to delay recognition to forms which already merit ecospecific status. It seems logical to draw the dividing line between ecotype and ecospecies at the level where the first bar to crossing is imposed which is not purely concerned with habitat-preference. The bar may be mechanical, physiological or operate at meiosis but it marks the initiation of *reproductive* isolation and, therefore, the achievement of ecospecific status. Mayr (1948), has emphasized that mechanisms which prevent crossing and those which tend to reduce the success of crosses should not be arbitrarily separated.

It is interesting that such an argument forms the basis of the *taxonomic* species-concept of Hutchinson, Silow, and Stephens (1947, p. 12) who accord specific rank in *Gossypium* to "all groups whose integrity is maintained by a real genetic barrier, whether this operates by preventing crossing, causing sterility in the F_1 hybrid, or by leading to genotypic disintegration in later generations."

Testing for reproductive isolation

An adequate test for out-breeding species might be this. The forms should be assembled in an experimental garden where the ecological factors which separate them in nature will be, as nearly as possible, eliminated. Care should be taken that any necessary pollinating insects are available (so that it would be a great advantage for the site of the test to be in the same region as that in which the forms occur naturally). If, then, there are any genetically determined features which prevent the free flow of genes between the forms but, at the same time, permit such a flow within the limits of each form, then those forms may be considered to be more or less reproductively isolated and therefore qualify at least as ecospecies. The nearest approach to this idealized set-up which I have yet seen is in the system of "isolation plots" developed by Clausen, Keck, and Hiesey (1940, 1945).

Mather (1947) with *Antirrhinum* and Grant (1949) with *Gilia*, have demonstrated practically the existence of what Grant has called "ethological isolation," where selective visitation by insect pollinators significantly reduces the incidence of interspecific pollination, and ascribe the insects' discrimination to differences in floral characters. Hybrids are found

between species of *Geum* whose areas overlap in Poland (Gajewski, 1949) but the species are kept distinct, even when there is complete lack of incompatibility and hybrid sterility barriers by "ecological differences, different times of flowering and failure of pollen transfer by insects." *Melandrium dioicum* (L.) Coss. and Germ. and *M. album* (Mill.) Garcke are separated to some extent by hybrid sterility (Åkerlund, 1933; Baker, 1950) but there is an additional separation of these campions by slight differences in phenology, in structure and time of opening of the flowers (with consequent differences in the chief pollinating insects) and by certation effects (Baker, 1945).

Inbreeding species present much more difficulty and it is not easy to visualize any adequate, comparable test. It is also true that the positions of habitually self-pollinated forms in the hierarchy from ecotype to comparium may be indefinite. Very closely related inbreeding forms may be as effectively isolated from each other (even when they are sympatric) as any ecospecies or higher category of outbreeding plant. Furthermore, the same degree of evolutionary divergence will not necessarily produce the same amount of hybrid incapacity when inbreeders are artificially crossed as when a similar action is performed with outbreeders (cf. Darlington and Mather, 1949). Consideration of the genera *Triticum, Avena, Nicotiana,* and the sub-genus *Euoenothera* will show at once that, apart from the inbreeding mechanism itself, bars to crossing are noticeably few.

It may be that it will prove impossible to fit the terms ecotype, ecospecies, etc., to habitually inbreeding forms for the same reasons as make unsatisfactory the application of the terms to apomictic forms (cf. Turesson, 1929; Gustafsson, 1947). Indeed there is considerable similarity between reproductive conditions in inbreeders and in apomicts. It may also be that it will never be possible to study with complete adequacy the isolation between plant forms if such an investigation must be conducted in the artificial environment of an experimental garden. Natural adaptation and natural isolation depend upon the interaction of each of the forms with the whole environment and it is as difficult to draw a narrow line of demarcation between "ecological" and "genetical" forms of isolation as it is to separate the "ecological" and "geographical." Nevertheless, the amount of information which the experimental culture of plant forms provides is so considerable that progress in this field can give us not only the information upon which to base our "special" classification but also can help us towards the "omega" taxonomy which Turrill (1938*a*, *b*) has visualized as the taxonomists' Holy Grail.

Appendix I

Definitions of the Ecospecies

Turesson (1922). ". . . the Linnean species or genotype compounds as they are realized in nature."

Turesson (1929). "An amphimict-population the constituents of which in nature produce vital and fertile descendants with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population."

Gregor, Davey, and Lang (1936). "A group also distinguished by morphological, physiological or cytological characters, or a combination thereof; separated from other parts of its coenospecies by restricted interfertility or by failure of hybrids to establish themselves in Nature."

Gregor (1939). ". . . a population with an inherently low capacity for exchanging genes with other populations of its coenospecies."

Clausen, Keck, and Hiesey (1939). ". . . if crossed, their hybrids are partially sterile, whereby non-viable sex cells are eliminated, or the second generation of offspring is weak; most often both these conditions obtain."

Clausen, Keck, and Hiesey (1940).

". . . a group of plants within the coenospecies whose members are able to exchange their genes without detriment to the offspring. Ecospecies are separated from one another by internal barriers that prevent such free interchange."

Cain (1944). "An amphimict population with vital and fertile descendants, but with reduced fertility or not readily crossed with other members of the coenospecies."

Clausen, Keck, and Hiesey (1945). ". . . all the ecotypes genetically so related that they are able to exchange genes freely without loss of fertility or vigor in the offspring."

Valentine (1948). ". . . species are ecospecies of a coenospecies when exchange of genes can take place between them, but when the exchange under either natural or artificial conditions is limited in some way."

Valentine (1949). "*g*-ecospecies. Groups with the same chromosome number between which there are well-defined morphological, ecological and geographical differences and which, under artificial or natural conditions are capable of only limited gene-exchange."

"*a*-ecospecies. Groups differing in chromosome number between which there are well-defined ecological and geographical differences and which are capable of only limited gene-exchange."

Darlington and Mather (1949). "ECO–SPECIES, capable of genetic recombination with other similar units, but liable to reduced fitness or fertility from it."

Summary

The unsuitability of the taxonomic species as a "unit of evolution" is emphasized and it is believed that for many problems in "micro-evolution" use of the categories of the "special" classification of biosystematics is preferable, although they are not as useful as a "general" classification in tracing phylogeny. The time has therefore come for an increased measure of agreement in the use of such terms as ecospecies and recent opinions and trends are discussed while a collection of published definitions is appended. An examination is made of the genetical criteria of ecospecific distinction. The development of hybrid incapacity is considered to occur in too irregular a manner to provide the only criterion and it is proposed that the dividing line between ecotype and ecospecies should be drawn at the level where the first bar to crossing is imposed which is not purely concerned with habitat-preference. Suggestions are made as to the manner in which tests for such barriers may be made.

After the completion of this manuscript, a reprint of Professor H. L. Mason's paper "Taxonomy, Systematic Botany and Biosystematics", (Madroño, **10**, 193–208, 1950) was received. As this journal is not normally available to me, this excellent and, in some ways, complementary paper had not been seen. It can be recommended to all those interested in clear thinking about taxonomy.

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PHYLOGENETIC STUDIES IN *EUOENOTHERA*[1]

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INTRODUCTION

For a number of years *Oenothera* has been the object of extensive studies utilizing the cytological and genetical peculiarities of the genus to provide an understanding of phylogenetic relationships within the group.[2] The present study, concerned with the cytogenetic analysis of certain races[3] of *Euoenothera* from the southeastern United States, represents one contribution to the reconstruction of the phylogenetic history of the group.

The North American euoenotheras belong to two principal cytogenetic types; on the one hand, races occurring primarily in California and Mexico are characterized by seven bivalents at meiosis, open-pollinated flowers, and the absence of lethals. The majority of euoenotheras occurring throughout the central and eastern United States, however, exhibit a circle of fourteen chromosomes at meiosis, balanced lethals, and a self-pollinating habit. Cytogenetic analysis of collections from many parts of the range of this latter group has shown it to be composed of many races differing with respect to the end arrangement of the chromosome sets or "complexes" which they carry. Although there occur many isolated races each composed of two complexes with dissimilar end arrangements, most of these races can nevertheless be grouped into certain broad categories on the basis of similarities in the segmental arrangement of their complexes. Furthermore, these categories are characterized in a general way by distinctive phenotypic features. These groups have been described by Cleland, 1949. For purposes of this discussion, only three of these need be mentioned here, namely:

Hookeris—These include the California and some Mexican races; they show seven pairs of chromosomes at meiosis and possess large, open-pollinated flowers. The segmental arrangement most commonly encountered in this group is: 1·2 3·4 5·6 7·10 9·8 11·12 13·14. This arrangement is considered to be ancestral for the euoenotheras.

Strigosas—These races range from the Rocky Mountains east to the Mississippi Valley and northwestward to the Pacific Coast. In appearance they are thick-leaved, grayish, with appressed pubescence; the two complexes have similar phenotypic effects. The alpha complexes (transmitted through the egg) are similar to each other in segmental arrangement; the beta complexes (transmitted through the pollen) are also similar to each other. The alpha complexes are very different in segmental arrangement from the beta complexes, however, although both are related to the ancestral arrangement, differing from the latter by about three interchanges on the average.

Biennis group 1—These are forms with broad, thin, crinkly leaves occurring from the Ozark region eastward through the Alleghenies to the Atlantic Coast in the region of Virginia; the distinctive phenotype of the group is carried by the alpha complexes. The beta complexes are typi-

[1] This paper is from a doctoral thesis submitted to Indiana University in June, 1950. The study was made possible through grants from the Rockefeller Foundation and Indiana University to Dr. R. E. Cleland for research in *Oenothera* cytogenetics. The author is indebted to Dr. Cleland for guidance and encouragement throughout this investigation.

[2] For a summary of these studies see Cleland, 1949.

[3] The term "race" indicates a line of descent more or less isolated from other lines of descent by the self-pollinating habit. A collection is a sample from the race.

cal *strigosa*-like complexes, which are, however, rather completely masked in the races themselves. Most of the alpha complexes of this group are only one interchange removed from the ancestral arrangement. The beta complexes are more closely related to the beta strigosas.

In the earlier work few collections from the southeastern United States had been analyzed cytogenetically; the results indicated the presence in this region of several types whose relationships were not obvious. The present investigation was undertaken to bring additional collections into the picture in order to determine the relationships of the southeastern euoenotheras.

Materials and Methods

The new races which have been analyzed in this study are listed in table I. Each of these was hybridized with a series of "standard" races, whose complexes were known in regard to segmental arrangement and the phenotypic characters which they produced. Determination of the meiotic chromosomal configurations of the hybrids provided the data from which the segmental arrangements of the complexes occurring in the new races were worked out. All cytological material was prepared according to the schedule described by Hecht, 1950. From analysis of the hybrid phenotypes, it was possible to determine the phenotypic characters which the new complexes produce.

Results

The newly determined segmental arrangements of the complexes studied are listed in table II. Limitations of space prohibit presentation of the hybrid chromosomal configurations as well as the reasoning which was used in working out these segmental arrangements. Descriptions of each race are also omitted. The complete cytological data and analysis along with the descriptions of the races are available in the thesis at the Indiana University library. The pertinent morphological features of the races and their component complexes must be mentioned

Table I. *New races included in the present study*

Race	Source	Collector	Year	Chromosome configuration
Alabama	University of Alabama campus, University, Ala.	R. M. Harper	1947	7 pairs
Athens A	11 miles north of Athens, Jackson Co., Georgia	A. Cronquist	1947	⊙ 14
Athens B	11 miles north of Athens, Jackson Co., Georgia	A. Cronquist	1947	⊙ 14
Athens C	11 miles north of Athens, Jackson Co., Georgia	A. Cronquist	1947	⊙ 14
Athens D	11 miles north of Athens, Jackson Co., Georgia	A. Cronquist	1947	⊙ 14
Biloxi	Biloxi, Miss.	P. A. Munz	1935	⊙ 14
Citronelle	Citronelle, Mobile Co., Ala.	P. A. Munz	1935	⊙ 14
Tuscaloosa A	Roadside east of Tuscaloosa, Ala.	B. Williams	1946	⊙ 14
Tuscaloosa B	Tuscaloosa, Ala.	B. Williams	1946	⊙ 14
Tuscaloosa C	Tuscaloosa, Ala.	R. M. Harper	1947	⊙ 14
Tensaw	Tensaw, Ala.	P. A. Munz	1938	⊙ 14

TABLE II. *Segmental arrangements of complexes in southeastern euoenotheras and their relatives*

Alpha and haplo-complexes							
**neo-acuens*	1.13	3.2	5.6	7.10	9.8	11.12	4.14
**acuens*	1.4	3.2	5.6	7.10	9.8	11.12	13.14
**α Biloxi*	1.2	3.4	5.10	7.6	9.8	11.12	13.14
*[h]*Dixie Landing*	1.2	3.4	5.6	7.10	9.8	11.12	13.14
[h]*Alabama*	1.2	3.4	5.6	7.10	9.8	11.12	13.14
α Tuscaloosa A	1.2	3.4	5.14	7.10	9.8	11.12	13.6
α Tuscaloosa B	1.2	3.4	5.14	7.10	9.8	11.12	13.6
α Tuscaloosa C	1.2	3.4	5.14	7.10	9.8	11.12	13.6
α Tensaw	1.2	3.4	5.14	7.10	9.8	11.12	13.6
α Athens B	1.2	3.4	5.14	7.10	9.8	11.12	13.6
α Athens D	1.2	3.4	5.14	7.10	9.8	11.12	13.6
**α Citronelle*	1.2	3.4	5.14	7.9	8.10	11.12	13.6
α Athens A	1.4	3.10	5.13	7.2	9.8	11.12	14.6
α Athens C	1.4	3.10	5.13	7.2	9.8	11.12	14.6
Beta complexes							
**truncans*	1.13	3.7	5.2	4.6	9.14	11.10	8.12
β Athens A	1.13	3.7	5.2	4.6	9.14	11.10	8.12
β Athens B	1.13	3.7	5.2	4.6	9.14	11.10	8.12
β Athens D	1.13	3.7	5.2	4.6	9.14	11.10	8.12
**β Warrenton*	1.13	3.7	5.2	4.6	9.14	11.10	8.12
**β LaCrosse*	1.13	3.6	5.2	7.4	9.14	11.10	8.12
**β Magnolia*	1.13	3.9	5.2	4.6	7.14	11.10	8.12
β Athens C	1.13	3.6	5.7	4.8	9.14	11.10	12.2
β Tuscaloosa A	1.13	3.2	5.7	4.8	9.12	11.10	14.6
β Tuscaloosa B	1.4	3.7	5.11	6.10	9.2	8.12	13.14
β Tuscaloosa C	1.4	3.7	5.11	6.10	9.2	8.12	13.14
β Tensaw	1.4	3.7	5.11	6.10	9.2	8.12	13.14
β Citronelle	1.4	3.13	5.9	7.2	11.6	8.12	10.14
β Biloxi	1.10	3.5	7.14	9.6	11.2	8.12	13.4
Complexes with arrangements related to the above complexes							
**β Rich Mountain*	1.4	3.7	5.11	6.10	9.2	8.12	13.14
**β Birch Tree 1*	1.4	3.13	5.7	6.11	9.10	8.12	14.2
**β Birch Tree 2*	1.13	3.2	5.7	4.12	9.6	11.10	8.14
**α Gothenburg*	1.10	3.12	5.8	7.2	9.6	11.4	13.14
Most common alpha *biennis* group 1 arrangement	1.2	3.4	5.14	7.10	9.8	11.12	13.6

* Determined in earlier studies.

in the discussion of their relationships which follows; it therefore seems superfluous to present them here also.

DISCUSSION

In these studies similarity in segmental arrangement is taken as the primary clue to phylogenetic affinity. Inspection of table II reveals that a number of the complexes are identical in segmental arrangement, and a close similarity exists between others. These similarities, when correlated with morphological and geographical data suggest that the southeastern euoenotheras should be classified into two primary groups. The first group (I) consists of races which show both segmental and morphological affinities to the *biennis* group 1 races. This group may be subdivided into two series one of which (a) consists of races from Alabama which are more or less identical morphologically with the midwestern *biennis* group 1; the other series (b) includes forms from

Georgia, which, although *biennis*-like, possess narrower leaves and a less branched habit than is characteristic of the typical *biennis* group 1 races. The second major group (II) includes the large-flowered, open pollinated, narrow-leaved forms which have been known to most botanists as *Oe. grandiflora* Ait. In addition, one race, collected at Biloxi, Mississippi, cannot be placed in either of the major groups, although it shows a distinct affinity to the *grandiflora* group.

In the following presentation, each of these groups will be dealt with separately. The cytological and morphological features which characterize the races belonging to a specific group as well as their geographical distribution will be summarized. The phylogenetic significance of these data is then discussed in the case of each group.

I. (a) Biennis races from Alabama

The three Tuscaloosa races, *Tensaw,* and *Citronelle* belong in this category. These races possess the following phenotypic characters: moderately broad, dark to light green, somewhat crinkled, moderately thick leaves with erect to suberect hairs; stems with a moderate to strong basal color; usually a well developed central shoot with considerable branching; small, self-pollinated flowers. The races *Tuscaloosa B* and *C,* and *Tensaw* also have red leaf margins, stem tips, hypanthia, and cones, and are almost identical in appearance. Green leaf margins, stem tips, hypanthia, and bud cones readily distinguish *Tuscaloosa A* from these races. *Citronelle,* which is the least typical member of this group, has brilliantly reddened stem tips, but green leaf margins, hypanthia, and bud cones; it further differs from the others in possessing somewhat narrower leaves and a less pronounced central shoot tendency. Each of these races is a complex heterozygote with a circle of 14 chromosomes at meiosis.

Alpha complexes. With the exception of ***alpha Citronelle,*** all of the alpha complexes of this group are identical in segmental arrangement. Of especial interest is the fact that this particular arrangement is characteristic of the alpha *biennis* group 1 complexes. *Alpha Citronelle,* which does not possess this same arrangement, is however, only one interchange removed from it. Instead of having 7·10 and 9·8, it has 7·9 and 8·10. From the standpoint of segmental arrangement, therefore, the alpha complexes of this series of races show the highest degree of relationship, not only to each other, but also to the great majority of the alpha *biennis* 1 complexes.

The phenotypic effects produced by *alpha Tuscaloosa A, B,* and *C, alpha Tensaw,* and ***alpha Citronelle*** are essentially *biennis*-like, although they may differ in minor characteristics. These complexes, in general, carry factors for fairly broad, dark green, somewhat crinkled, thin leaves, considerable branching, rather slender, tapered bud cones, and erect bracts. The similarity in regard to phenotypic effect of these complexes to those of the alpha *biennis* group 1 is striking; these phenotypic effects are all more or less characteristic of the alpha *biennis* 1 complexes. There is, therefore, no segmental or phenotypic distinction between the alpha complexes of this southern group and those of the midwestern *biennis* 1 category.

Beta complexes. The segmental arrangements of three beta complexes, *beta Tuscaloosa B* and *C,* and *beta Tensaw* are identical. This particular arrangement also occurs in the beta complex of *Rich Mountain,* a *biennis* group 1 race from Arkansas. The remaining two races, *Tuscaloosa A* and *Citronelle,* have beta complexes which are a minimum of six and four interchanges removed, respectively, from the *beta Rich Mountain* arrangement. These beta complexes, however, show close segmental relationships to other beta *biennis* 1 complexes; *beta Citronelle* is only two interchanges removed from *beta Birch Tree 1,* while *beta Tuscaloosa A* is two interchanges distant

from *beta Birch Tree 2*. Both Birch Tree races occur in southern Missouri and belong to the *biennis* group 1. Thus, although the beta complexes of these Alabama races lack the degree of segmental uniformity shown by the alpha complexes, they do, nevertheless, show affinities to the beta *biennis* 1 complexes, so far as segmental arrangement is concerned.

The morphological characters which are produced by the *beta Tuscaloosa A, B,* and *C, Tensaw,* and *Citronelle* complexes are essentially *strigosa*-like. These complexes produce narrow, gray green, thick leaves with appressed pubescence, a strict habit with little branching, flaring bracts, and thick, rather short bud cones. The same morphological features characterize the beta *biennis* 1 complexes. The morphological similarity of these two groups of beta complexes further strengthens the conviction that they are closely related.

Geographical distribution. Those midwestern *biennis* group 1 races which show the closest affinities to the Alabama *biennis* forms occur in Arkansas and southern Missouri. The Tuscaloosa races were collected in west central Alabama, while *Tensaw* and *Citronelle* were obtained from two distinct localities in southwestern Alabama. Hence, the range of the Alabama races can be considered as more or less continuous with that of the midwestern forms. Whether similar forms occur farther east in Georgia, Florida, and South Carolina cannot yet be determined in the absence of more numerous collections from this area.

The Alabama *biennis* races are linked to their southern habitat by two distinctive features; they do not form an appreciable rosette,[4] nor do they bloom until late in the season. They are short day plants.

Relationships of the Alabama biennis forms. The foregoing evidence appears overwhelmingly in favor of interpreting these races as typical *biennis* group 1 forms. The races are *biennis* in appearance; they possess alpha complexes which carry factors for a *biennis* phenotype, and these are associated with beta complexes producing *strigosa* characters. Segmentally, the alpha complexes are identical, or in one case only one interchange removed, with the segmental arrangement characteristic of the midwestern alpha *biennis* 1 complexes. The beta complexes, although in only three cases segmentally identical with one of the midwestern beta *biennis* arrangements, nevertheless, show close relationships to the latter group. In addition, the range of the southern forms is contiguous with that of the midwestern races. For these reasons, the Alabama *biennis* forms are considered to belong to the *biennis* group 1 category and their presence in Alabama constitutes an extension of the range of *biennis* group 1.

I. (b) Biennis-like races from Georgia

Included in this category are four races collected near Athens, Georgia. These small flowered, self-pollinated forms, although more or less *biennis*-like in appearance, are separated from the Alabama *biennis* group because they display certain modifications of the typical *biennis* phenotype. They possess somewhat narrower, lighter green leaves, longer internodes, a stricter habit, and are less branched. Each race is a complex heterozygote with a circle of 14 chromosomes at meiosis.

Alpha complexes. Alpha Athens B and *D* are identical in segmental arrangement with the typical alpha *biennis* 1 complexes. *Alpha Athens A* and *C,* which are identical in segmental arrangement, are only three interchanges removed from the most common alpha *biennis* 1 arrangement. Segmentally, these alpha complexes, therefore, show a distinct affinity to the alpha *biennis* group 1.

In regard to phenotypic effect, the alpha Athens complexes produce characters, which, while *biennis*-like, tend to

[4] At least under garden conditions in Indiana, in contrast to the midwestern *biennis* group 1 races.

lean toward a type with slightly narrower, less crinkled, somewhat thicker leaves.

Beta complexes. The phenotypic effects produced by the four beta Athens complexes are similar; these include narrow, short, grayish green, strongly wavy, thick leaves, a strict habit with little branching, flared bracts, and a rather stout, thick-skinned bud cone. Although the general effect is *strigosa*-like, it differs from a typical *strigosa* phenotype in the shorter, stiffer, narrower leaves. These differences are in part responsible for the deviation of these races from a typical *biennis* group 1 phenotype.

Although the alpha complex of *Athens A* is identical segmentally with the alpha of *Athens C*, the beta complex of *Athens A* is identical in segmental arrangement with *beta Athens B* and *D*. The segmental arrangement of *beta Athens C*, however, is three interchanges removed from that of *beta Athens A, B,* and *D*.

It will be noted (Table II) that the arrangement found in the latter three complexes occurs rather widely among races from the southeast as well as from the eastern part of the *biennis* group 1 range. This arrangement was first found in the *truncans* complex of the *grandiflora* of deVries, a race which will be discussed later in connection with the *grandiflora* group. Two races occurring in Virginia, *Warrenton* and *Charlottesville*, each possess one complex with the *truncans* arrangement. In the former race the beta complex, in the latter, the alpha complex exhibits this arrangement. In addition, the arrangements of the beta complexes of *LaCrosse*, a race from Virginia, and *Magnolia*, a race from Kentucky, are each one interchange removed from the *truncans* arrangement.

Relationships of the Athens races. The characteristics of the Athens races outlined in the foregoing paragraphs suggest two tentative conclusions in regard to the phylogenetic affinities of this group. First, the Athens group shows a distinct relationship to the *biennis* group 1. On the other hand, the widespread occurrence of complexes with the *truncans* or modified *truncans* arrangement suggests that the races which carry such complexes represent a distinct phylogenetic grouping to which the Athens races belong.

Considerable evidence exists which relates the Athens forms to *biennis* group 1. The Athens races are *biennis*-like in appearance. They possess alpha complexes which produce *biennis*-like phenotypes and which have segmental arrangements identical with, or closely related to, the typical alpha *biennis* 1 arrangement. The beta complexes, although at least four interchanges removed from the typical beta *biennis* 1 arrangements, produce *strigosa*-like characters which are somewhat similar to those produced by typical beta *biennis* 1 complexes. Furthermore, the Athens races occur toward the margins of the *biennis* group 1 range. The distinction between the Athens races and the *biennis* group 1 forms depends, therefore, primarily on the rather limited phenotypic and segmental differences between the beta complexes of the two groups.

The fact that the modified *strigosa* phenotype found in the beta Athens complexes is correlated with a distinctive segmental arrangement suggests that these races belong to a phylogenetic entity which is distinct from the *biennis* group 1. The races *Warrenton, LaCrosse,* and *Magnolia,* which also possess beta complexes showing the *truncans* or modified *truncans* arrangement, exhibit certain phenotypic similarities to the Athens races. They are, like the Athens races, narrow leaved, *biennis*-like in appearance; their alpha complexes belong to the alpha *biennis* group 1, both from the standpoint of phenotype as well as segmental arrangement. The beta complexes, like the beta Athens complexes, although similar to the beta *biennis* 1 complexes in phenotype, do not produce a typical *strigosa* phenotype. Moreover, *Warrenton, LaCrosse,* and *Magnolia* occur toward the eastern limits of the *biennis* group 1 range.

In the light of the above facts, *Warrenton, LaCrosse, Magnolia,* and the Athens races are considered to be outlying *biennis* group 1 forms, which have become differentiated from the typical *biennis* 1 type both phenotypically and segmentally. The *truncans* arrangement, arising through a series of interchanges among the beta *biennis* 1 complexes and concurrently accumulating genetic factors having adaptive value in the southeastern area, has become characteristic of a population of *Euoenothera* in this region. The extent to which the *truncans* arrangement is distributed among the southeastern *biennis*-like forms can only be determined by the analysis of additional races from this area. More knowledge concerning the distribution of this arrangement may also throw light on its manner of origin among the beta *biennis* 1 arrangements.

It is of interest to note that there is also some evidence of relationship between the Athens races and the Alabama *biennis* group. Apart from the segmental and phenotypic similarity of the alpha complexes of these two groups, relationship is also indicated by the fact that *beta Tuscaloosa A* has a segmental arrangement only three interchanges removed from *beta Athens A,* and only two interchanges removed from *beta Athens C.* It will be remembered that *beta Tuscaloosa A* differs from the other two beta Tuscaloosa complexes in phenotype and segmental arrangement. This race may represent an intermediate form between the typical *biennis* forms and those, like the Athens group, which have become modified. It is difficult to determine, however, whether such an apparently intermediate form does actually represent a stage in the sequence of development of one phylogenetic grouping from another.

II. Grandiflora group [5]

This southern group is represented in our collections by *Dixie Landing, Alabama,* and the *grandiflora* of deVries. These races are characterized by large, open-pollinated flowers, rather narrow, dark to light green, smooth leaves, few short, erect hairs, erect bracts, and glabrous, green capsules. Unlike other forms of *Euoenothera,* the grandifloras have distinctly fragrant flowers. Other characters may differ from race to race so that each race has a distinctive appearance. For example, *Dixie Landing* has deeply lobed leaves and a spreading habit. *Alabama,* on the other hand, has evenly and finely toothed leaf margins and exhibits a low, compact habit unlike that found in any other *Euoenothera* of our collection. *Dixie Landing* and *Alabama* are races with all pairing chromosomes and no lethals. *Grandiflora* (deVries), however, is a complex heterozygote with a circle of 14 chromosomes and balanced lethals.[6]

Both [h]*Dixie Landing* [7] and [h]*Alabama* possess the segmental arrangement which is considered ancestral among the North American euoenotheras, namely, 1·2 3·4 5·6 7·10 9·8 11·12 13·14. Since these races are homozygous, the phenotypic effects of their complexes are fully shown in the races themselves.

On the other hand, *grandiflora* (deVries), a complex heterozygote is com-

[5] The name *grandiflora* is used to designate a phylogenetic grouping except in those cases where it is followed by "(deVries)" when it applies to the race collected by deVries. As the discussion will reveal, this phylogenetic grouping is not identical with *Oe. grandiflora* Ait., since the latter may include certain types excluded from the former on the basis of cytogenetic characteristics.

[6] The *grandiflora* of deVries when originally received in our collection had ⊙ 14, its complexes being *acuens* and *truncans* (Hoeppner and Renner, 1928; Gerhard, 1929). As a result of interchange occurring in the experimental garden, the race as now grown has ⊙ 12, 1 pair; the ⊙ 14 form has been lost. The complex resulting from this interchange is called *neo-acuens,* since it is one interchange removed from *acuens.* The possible origin of *neo-acuens* is discussed by Cleland, 1950. For the sake of simplicity, *grandiflora* (deVries) will be considered as a ⊙ 14 form in the current discussion.

[7] The superscript "h" is used before a complex which is present in double dose in a complex homozygote.

posed of the two complexes, *acuens* and *truncans*. The *acuens* arrangement is one interchange removed from the ancestral arrangement, having 1·4 and 3·2 instead of 1·2 and 3·4. *Acuens* is, therefore, closely related segmentally to [h]*Dixie Landing* and [h]*Alabama*. Furthermore, *acuens* produces a phenotype characterized by large flowers, narrow leaves, and erect bracts which is similar to that of the homozygous *grandiflora* races. The *truncans* complex, although producing a *grandiflora* phenotype, is, nevertheless, far removed segmentally from the ancestral arrangement.

Since the *truncans* arrangement has been encountered in the Athens races, it appears that *grandiflora* (deVries) is a hybrid between a homozygous *grandiflora* race such as *Dixie Landing* or *Alabama* and a race similar to the Athens forms, the former contributing the *acuens* complex, the latter the *truncans* complex. That such a hybrid could occur is not unlikely, since Bartlett and deVries (1912) have described numerous *biennis*-like types growing together with the grandifloras in the native habitat of the latter group. This explanation unfortunately has one difficulty; *truncans* produces a phenotype very similar to that of *acuens* and not the same phenotype associated with the *truncans* or modified *truncans* arrangement in the Athens races, *Warrenton, LaCrosse,* and *Magnolia*. The beta complexes of the latter races do share in common with the *truncans* of *grandiflora* (deVries) certain features such as narrow leaves, strict habit, and flaring bracts. *Truncans,* however, produces darker green, less wavy, thinner leaves and large flowers in contrast to the gray green, thick, wavy leaves and small flowers of the other complexes. If *truncans* and the other complexes showing the *truncans* or slightly modified arrangements are as closely related as similarity in segmental arrangement seems to indicate, then an explanation for a modification to the *truncans* phenotype is in order. The factor for large flowers could have easily been acquired from *acuens* as a result of crossing over, since this gene, located near the end of the chromosome, shows 50 per cent crossing over (Emerson and Sturtevant, 1932). There is no evidence, however, as to whether the other *grandiflora* characters could have been transferred to *truncans* in the same manner. Whatever the explanation, it seems probable that *grandiflora* (deVries) is not typical, at least cytogenetically, of the *grandiflora* population as it exists in nature. The true grandifloras appear to be complex homozygotes; the *grandiflora* of deVries is a complex heterozygote with one *grandiflora* complex and another complex which is phenotypically *grandiflora* but segmentally of a different origin. Further work will be necessary before the affinities of *truncans* are understood.

Geographical distribution of the grandifloras. William Bartram first observed *Oe. grandiflora* Ait. in 1778, when he found it growing at Dixie Landing on the Alabama River near Tensaw, Alabama.[8] This locality was rediscovered by Tracey in 1904 (Bartlett and deVries, 1912). The race, *Dixie Landing,* although collected on the University of Alabama campus where it was under cultivation, is known to have descended from plants obtained from the Dixie Landing habitat. Whether *Alabama,* which was also obtained on the University of Alabama campus, was originally collected at Dixie Landing is not known; it seems likely, however, that this is the case, since there is no record that the *grandiflora* types are also native to the Tuscaloosa area. The other *grandiflora* race in our collection, *grandiflora* (deVries) was collected at Castleberry, Alabama, not far from Tensaw. Thus the *grandiflora* forms appear to be native to a single locality in southern Alabama. There is at present no evidence that the grandifloras occur in any other area in the Southeast, although an intensive field survey of the entire

[8] Bartram, William. The travels of William Bartram. Edited by Mark van Doren. New York, 1940.

region might reveal additional habitats of these forms. Even if the grandifloras were found elsewhere, the possibility that they represent escapes from cultivation would have to be considered. Gray's Manual states that the grandifloras were formerly cultivated and occur occasionally as escapes.

Relationships of the grandifloras. What is, then, the position of the grandifloras in the phylogenetic pattern of the North American euoenotheras? The limited distribution of the grandifloras has been interpreted by Bartlett [9] as evidence that they represent the remains of an older, once widely distributed population. This hypothesis finds support in a number of facts. In the first place, these forms show an ancestral segmental arrangement; from this standpoint they must be considered primitive. The phenotypic character of the grandifloras except for the large, open-pollinated flowers is, however, quite different from that found among the hookeris, a fact which would appear to deny the close relationship indicated by the cytological evidence. On the other hand, there is a possibility that the grandifloras are relics of a population which spread from the Southwest at a time when conditions were considerably moister than they are at the present time. There is some evidence (Antevs, 1928; Mayr, 1945) that during the Pleistocene period the climate throughout the Southwest was more generally moist than at present and that those regions which are now deserts may have supported a mesophytic flora. The grandifloras, which are mesophytic in character, may have been a segment of such a population which ranged throughout this area and spread southeastward. As the climate of the Southwest changed from a mesophytic to a xerophytic one, those variants which were better adapted to the drier climate survived in the Southwest. In the Southeast, where the climate remained moist, the mesophytic types persisted. The isolation which was thus established between the two groups, provided an opportunity for further differentiation and divergence of the two groups. The *grandiflora* races in our collection show considerable morphological variability; Bartlett and deVries (1912) have described seven different *grandiflora* types in regard to such characters as cone color, capsule length, pubescence, and leaf margins. Such variability is additional evidence that the grandifloras represent an older group of euoenotheras.

Why are the grandifloras confined to a single locality at present? What is the relationship of the grandifloras to the *biennis* forms which occur in the same and neighboring areas? From the standpoint of segmental arrangement, the *grandiflora* complexes are only one interchange removed from most of the alpha *biennis* 1 complexes, thus indicating a close relationship between these groups of complexes. This relationship is further substantiated by the phenotypic effects produced by the *grandiflora* and alpha *biennis* 1 complexes. The *grandiflora* complexes produce essentially a *biennis*-like phenotype except for their narrow leaves and large flowers; in fact, the grandifloras have been considered to be merely a variety of the *biennis* type (Lindley, 1833). Furthermore, the alpha Athens complexes produce a phenotype which is more or less intermediate between a strong *biennis* and a *grandiflora* type. These alpha complexes carry factors for narrower, less crinkled leaves than found in the typical midwestern alpha *biennis* 1 complex. There is, therefore, both morphological and cytological evidence of relationship between the *grandiflora* and alpha *biennis* 1 complexes.

Such a relationship provides a clue to the possible origin of the alpha *biennis* 1 complexes. Cleland (1949), in discussing the origin of the alpha and beta *biennis* 1 complexes, states, "The beta complexes may be derived from the beta strigosas, but the origin of the alpha complexes is not so clear. They may represent an earlier indigenous population

[9] Conversation with Prof. H. H. Bartlett.

which crossed with the later invading strigosas." The evidence of both morphological and cytological affinity between the *grandiflora* and alpha *biennis* 1 complexes suggests that the grandifloras may represent a southern derivative, the alpha *biennis* 1 complexes a northern offshoot of the "earlier indigenous population" to which Cleland refers. If this population originally spread from the Southwest into the Midwest and East, it is probable that on the northern limits of its range it contacted the strigosas which were invading the Midwest from the Plains region. Hybridization occurring between the two groups then produced a *biennis* group 1 type. To the south segments of this same population became modified toward the *grandiflora* phenotype. Thus, through this earlier population it is possible to relate the alpha *biennis* 1 complexes to the grandifloras as well as to the ancestral California forms, an affinity indicated by the close similarity of the alpha *biennis* 1 arrangements to the ancestral arrangement.

This hypothesis at the same time provides an explanation for the decline in the geographical range of the grandifloras. With the development of ⊙ 14 *biennis* forms in the Midwest, the selective advantage generally attributed to the complex heterozygotes allowed these *biennis* forms to supplant the indigenous races in the Midwest and to invade the southern area occupied by the grandifloras, for the most part supplanting them also. Thus, at the present time, the grandifloras survive in only one known locality, while the common *Euoenothera* in the South is essentially a *biennis* type. The grandifloras, therefore, comprise a morphologically distinct group of euoenotheras known to be native only near Tensaw, Alabama. They possess the ancestral segmental arrangement,[10] indicating relationship to the California euoenotheras. Such a relationship suggests the hypothesis that during earlier geologic periods a mesophytic population was distributed from California throughout the Southwest to the Southeast. With climatic changes in the Southwest to a xerophytic habitat, the mesophytic types such as *grandiflora* persisted only in the Southeast.

In the Midwest where the mesophytic population came into contact with the strigosas moving eastward from the Plains region, the *biennis* group 1 forms with a circle of 14 chromosomes originated, the alpha *biennis* 1 complexes being derived from this earlier population and the beta *biennis* 1 complexes from the beta strigosas. The increased survival value of these complex heterozygotes has allowed the successful extension of their range throughout the Midwest and into the Southeast. The grandifloras, on the other hand, where no longer able to maintain themselves in competition with the *biennis* races and now exist only as a relic population in one locality in Alabama.

III. Unclassified forms

Although the race *Biloxi,* collected at Biloxi, Mississippi, cannot be placed in either the southern *biennis* or the *grandiflora* category, it does show a definite relationship to the latter group. In appearance, *Biloxi* is a *grandiflora* form except for its small, self-pollinated flowers. It is a complex heterozygote with a circle of 14 chromosomes at meiosis.

Analysis of its complexes has revealed that the alpha complex carries the factors producing the *grandiflora* phenotype displayed by the race. In addition, the alpha complex possesses a segmental arrangement only one interchange removed from the ancestral arrangement found in the *grandiflora* complexes. Instead of 5·6 and 7·10, *alpha Biloxi* has 5·10 and 7·6. For these reasons, *alpha Biloxi* is classified as a *grandiflora* complex.

Beta Biloxi, however, produces a phenotypic effect which is typically *strigosa;*

[10] Since *grandiflora* (deVries) does not appear to be representative of the grandifloras, at least cytogenetically, discussion of the *grandiflora* relationships applies only to the homozygous *grandiflora* races.

it carries factors for gray green, wavy, thick leaves, appressed pubescence, flared bracts, and stout buds. It is of especial interest that these characters are almost completely masked by the *grandiflora* characters of the alpha complex. In regard to segmental arrangement, *beta Biloxi* does not show a close affinity to any of the known complexes, with one exception, which produce a *strigosa* phenotype. It is only three interchanges removed from *alpha Gothenburg,* one of the alpha *strigosa* complexes from Nebraska, a fact which may turn out to have some significance. It should be noted, however, that *Biloxi* is the only collection from Mississippi which has been analyzed; moreover, no races from either Louisiana or Texas have been studied. Thus a relatively large area remains unknown which may contain a group of complexes of which *beta Biloxi* may be a member. *Biloxi* probably represents a hybrid between the *grandiflora* and an unknown Mississippi group. Professor S. M. Tracey, who rediscovered the *grandiflora* habitat in 1904, introduced these grandifloras into the Biloxi area.[11] These may have hybridized with forms native to Biloxi to produce complex heterozygotes of which our race is representative. A study of other Mississippi races will provide a test for the hypothesis that *Biloxi* is of recent hybrid origin.

With one exception, therefore, all of the southern euoenotheras so far analyzed fall into two principal phylogenetic groupings. The first of these is a group showing close *biennis* affinities, the Alabama members of which represent a southern extension of the Midwestern *biennis* group 1, while the Georgia members so far studied, contain beta complexes which have a distinctive segmental arrangement and a phenotype which is somewhat modified from the typical beta *biennis* 1 phenotype in the direction of *grandiflora.* Whether or not the latter category is representative of a widely distributed southern population showing a regional specificity in regard to segmental arrangement and phenotype can only be determined by the analysis of additional races from the South. As yet, our collection does not include forms from central and southern Georgia, Florida, South Carolina, and eastern North Carolina. A uniform sampling of this area will undoubtedly do much to clarify the status of the modified *biennis* forms such as the Athens races.

The other principal southern group, the *grandiflora* assemblage, is in all probability confined to a single locality in southern Alabama, and may represent the remains of an earlier population which was widely distributed throughout the Southeast. These forms are complex homozygotes, whose complexes show relationships both to the hookeris of California and to the midwestern alpha *biennis* group 1 complexes.

In conclusion, one may ask whether these phylogenetic groupings are useful taxonomic entities. The *grandiflora* group is certainly morphologically distinct enough to be treated as a separate taxonomic unit. Of the southern group which shows *biennis* affinities, the Alabama series is difficult to distinguish from the midwestern *biennis* group 1. To distinguish these forms purely on the basis of geographical distribution does not seem justified. On the other hand, the Georgia races, along with *Warrenton, LaCrosse,* and *Magnolia,* show narrow-leaved *biennis*-like phenotypes which differentiate them from the typical midwestern *biennis* group 1 forms. Whether these narrow-leaved forms constitute a useful taxonomic entity may be questionable, however, since the differences upon which such a category would be based are not great and have only been observed under standard conditions in the experimental garden. In nature, it is likely that environmental variations may tend to obscure these differences. Further study, involving field surveys, will first be necessary to determine whether the characteristic features of this group are consistently recognizable.

[11] Conversation with Prof. H. H. Bartlett.

Summary

The results of a cytogenetic analysis of ten races of *Euoenothera* from the southeastern United States are summarized. On the basis of evidence derived from studies of segmental arrangement, morphology, and geographical distribution, the relationships of these races are discussed.

The races from the southeastern United States which have been studied appear to fall into two major phylogenetic groupings. The first group, which shows relationships to the *biennis* group 1, includes (a) a series of races from Alabama which are identical with the midwestern *biennis* group 1, and (b) a series from Georgia, which, although *biennis*-like, shows characters which lean toward the *grandiflora* phenotype. The second major group consists of large-flowered, narrow-leaved forms which are called grandifloras. The race, *Biloxi*, although possessing one complex of the *grandiflora* type, cannot be classified in either of these groups.

The Georgia races are distinguished from the midwestern *biennis* group 1 primarily by their beta complexes, which differ somewhat from the beta *biennis* 1 complexes in phenotype, and which possess a distinctive segmental arrangement. These races are interpreted as modified *biennis* group 1 forms which appear to be particularly adapted to the Southeast.

The grandifloras appear to be native to a single locality in southern Alabama. Because the members of this group have all pairing chromosomes which possess the ancestral segmental arrangement also found in the *hookeri* group, the grandifloras are interpreted as a relic population from a once widely distributed population which originally spread from the Southwest.

On the basis of certain segmental and phenotypic similarities between the *grandiflora* and alpha *biennis* group 1 complexes, a hypothesis is suggested to account for the origin of the biennis group 1 forms through hybridization of an earlier population of which the grandifloras are a southern derivative, with *strigosa*-like races moving eastward from the northern Plains region.

Evidence is presented which indicates *Biloxi* is a hybrid between a *grandiflora* and a form occurring in Mississippi, which has not yet been analyzed but which may be related to the alpha strigosas.

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HETEROPLOIDY IN *SEDUM ROSEA* (L.) SCOP.

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INTRODUCTION

Cytotaxonomists have found many different chromosome numbers in the Crassulaceae. In several cases differences in chromosomes have provided valuable information concerning relationships within the family (cf. Baldwin, 1939; Uhl, 1948). Such criteria of relationship must be used with some caution, however, for in a growing number of instances heteroploidy has been found in morphologically similar plants. Eupolyploidy has been the commonest type of heteroploidy detected (cf. Baldwin, 1939, 1943), but there are also several cases of apparently intraspecific aneuploidy. *Sedum rosea* (L.) Scop. provides one of these.

Sedum rosea, as conceived by Berger (1930) and many other recent taxonomists, is a highly polymorphic, usually dioecious species that is widely distributed in the northern parts of North America and Eurasia. The taxonomy and synonymy are rather complicated, and distinct binomial combinations have been proposed by a number of authors for forms that other taxonomists include in the one species. Because of its dioecious, tetramerous flowers, Linnaeus kept the species apart from *Sedum* and created for it the genus *Rhodiola.* A number of modern taxonomists still recognize *Rhodiola* as a genus, but most recent students of *Sedum* (e.g., Praeger, 1921; Berger, 1930; Fröderström, 1930), are agreed that it is best subordinated to *Sedum,* possibly as a section (Berger). The latter treatment is followed here.

Previous workers have studied collections of *Sedum rosea* from Greenland through Europe and Asia to Japan. In all cases they have found gametic chromosome numbers of 11 or somatic numbers of 22. Levan (1933) found these numbers in *"Sedum Rhodiola* DC" (*S. rosea*) from Bohuslän, Sweden; Bodö, Norway; the Faeroe Islands; and the Altai Mountains of central Asia. One bivalent at meiosis in staminate plants was reported to be slightly heteromorphic and was presumed to be a sex-chromosome pair of the XY type.

Toyohuku (1935) studied *"Sedum Rhodiola,* var. *elongatum"* (*S. rosea,* var. *elongatum* (Led.) Maxim.) from the Japanese island of Hokkaido and reported $n = 11$ in staminate plants and $2n = 22$ in both staminate and pistillate plants. Later, publishing under the name of Soeda (1944), he confirmed his previous count and stated that the plants came from Mt. Teine, near Sapporo.

Recently, Sörenson and Westergaard (unpublished, see Löve and Löve, 1948) have found a somatic number of 22 in a plant of this species from northeastern Greenland.

The species (*sensu latiore*) is also widely distributed in the northern part of North America, from Alaska and Labrador south in the Rocky Mountains to Mexico (Berger) and to several localities in the eastern United States. In the latter area the species has a very discontinuous distribution, occurring only in relatively small isolated areas where the necessary environmental conditions are met. No previous reports of the chromosomes from North American localities have been published.

MATERIALS AND METHODS

Most of the plants studied are part of a large collection of *Sedum* assembled at Cornell by Prof. R. T. Clausen and, unless otherwise stated, were collected in

the wild by him. Some of the material was fixed in the wild; other plants were cultivated at Ithaca before being studied. Pressed specimens of most collections are in the Wiegand Herbarium of Cornell University.

Most of the collections were studied from aceto-carmine squash preparations of young anthers following fixation in a modification of Carnoy's fluid (3 parts chloroform, 2 parts absolute ethyl alcohol, 1 part glacial acetic acid). One collection (C4633) was sectioned and stained in crystal violet. After this method the chromosomes appear smaller than after aceto-carmine. Only staminate plants were studied and, in most cases, only one plant of a population. If possible, counts were made from microsporocytes at metaphase I of meiosis, but in a few cases somatic divisions in the young anther walls or root tips were the best stages available. Meiotic metaphases apparently occur only during the early forenoon.

Photomicrographs of representative collections were taken at about 2,000 × and are reproduced at the same magnification.

Observations and Discussion

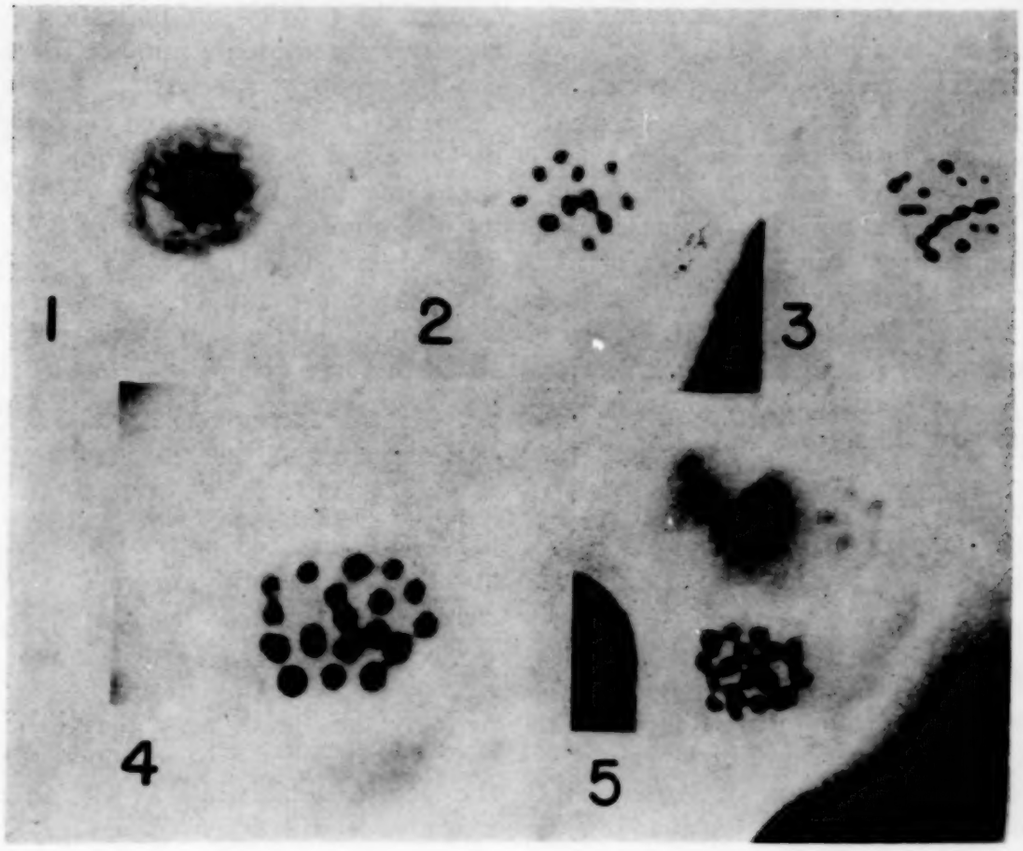
A list of plants studied and their chromosome numbers is given in table I. It is apparent that there are two chromosomal strains of *S. rosea* in North America. The 11-chromosome strain, as far as known now, appears to be confined to the northeast, whereas the 18-chromosome strain appears to have a wider distribution, occurring in central New York, in Minnesota, and in the West.

As may be seen from the photographs, the chromosomes of all collections are so small and so similar in appearance that it has not been possible to identify individuals and thus to compare the complements of the two strains. This applies to somatic as well as to meiotic chromosomes. Also, no heteromorphic bivalent, such as the one described by Levan (1933), has been found in any of these collections having either chromosome number, though meiosis was not seen in all collections. Soeda (1944) also stated that he was unable to detect heteromorphism in any bivalents in his material. It is quite likely that there is variation within *S. rosea* with respect to the presence and degree of differentiation of sex chromosomes, since the species is not completely dioecious and plants and populations having perfect flowers occur (e.g., C4633 here).

The species is highly polymorphic, exhibiting diversity in many morphological characters when populations from a number of different localities are compared. However, few, and perhaps none, of

Table I. *Chromosome numbers in* Sedum rosea (*L.*) *Scop.*

C48–46	Machias Seal Island, N. Brunswick, Canada (O. Hawksley)	n = 11
C7059	Mt. Horrid, near Rochester, Vt.	n = 11
C6815	Chittenango Falls, Madison Co., N. Y.	n = 11
C7050	Near Haines Falls, Greene Co., N. Y.	2n = 22
C7243	Ulster Co., N. Y.	n = 11 (Fig. 2), 2n = 22
C7031	Cliffs along Delaware River, below Millrift, Pike Co., Pa.	n = 11, 2n = 22
C6829	Delaware River, near Riegelsville, Bucks Co., Pa.	2n = 22
C7110	Cliffs along west shore of Seneca Lake, near Glenora, Yates Co., N. Y.	n = 18, 2n = 36
C41	Watkins Glen, Schuyler Co., N. Y. (W. Wilson)	n = 18 (Fig. 5)
C7026	Same locality	n = 18, 2n = 36
C7760	Cliffs along N. branch of Root River, south of Simpson, Olmstead Co., Minn.	n = 18
C7847	Rio Hondo Canyon, near Twining, Taos Co., N. Mex. (*S. polygamum* Rydb.)	n = 18
C4633	Sandia Mts., Bernalillo Co., N. Mex.	n = 18 (Fig. 3)
C7784	Middle Ridge of Sierra Blanca, Otero Co., N. Mex., about 3,000 m.	n = 18
C7792	Main peak of Sierra Blanca, Otero Co., N. Mex. (Topotype of *Rhodiola neomexicana* Britton.)	n = 18 (Fig. 4)
U215	Hutchinson Meadows, Fresno Co., Calif. (J. Rattenburg) about 2,900 m.	2n = 36 (±4)



Meiosis in microsporocytes of *Sedum rhodanthum* (fig. 1) and *S. rosea* (figs. 2–5), × 2,000. Figures 1–4 are first metaphase; figure 5 is second metaphase.

FIG. 1. C4654, n = 7.
FIG. 2. C7243, n = 11.
FIG. 3. C4633, n = 18.
FIG. 4. C7792. n = 18.
FIG. 5. C41, n = 18.

these differences appear to be consistently correlated with the difference in chromosome number. Although populations having the different chromosome numbers must be regarded as belonging to different genetic species, and although such populations must be reproductively isolated from one another, the weakness (absence?) of dependable morphological criteria for identifying the two chromosomal races may make their description or recognition as separate taxonomic species undesirable. Taxonomists do not agree in their treatments of situations of this sort. Professor Clausen is making a thorough taxonomic study of the various races of *S. rosea*. His results will be published separately.

In order to understand the origin of such different chromosome complements in a group of plants which look so much alike that they are widely considered a single species, it is necessary to know something about the chromosomes of related species. In North America *Sedum rhodanthum* Gray of the Rocky Mountain region is the only indigenous species of Section Rhodiola besides *S. rosea* (*sensu latiore*). *S. rhodanthum* has perfect flowers and is so different from *S. rosea* that Rose (Britton & Rose, 1903)—who also recognized *Rhodiola* as a genus—erected for it a separate monotypic genus, *Clementsia*. This genus, however, has not been widely accepted, and the modern tendency is to include the species within Section Rhodiola of *Sedum*. One collection has been studied: C4654, from the

San Francisco Mountains, Coconino Co., Arizona, has n = 7 (fig. 1).

The great majority of the species of Section Rhodiola are native to central Asia, and only one of these has been available in this study. U262, *Sedum dumulosum* Franch., a northern Chinese species obtained from cultivation, has n = 7. Berger (1930) included both *S. dumulosum* and *S. rhodanthum* in his Series Crassipedia but placed *S. rosea* in Series Rosea of the section. The chromosome numbers are in accord with this treatment.

Thus, in Section Rhodiola in North America, gametic chromosome numbers of 7, 11, and 18 are known. It is suggested that the basic chromosome number in the section may be 6, that plants with 7 were derived from diploids with 6, those with 11 from tetraploids with 12. If this is true, there are two ways the 18-chromosome strain of *S. rosea* could have evolved: (1) As a hexaploid with respect to an ancestral number of 6; (2) As an amphiploid between forms of *S. rosea* with 11 and some parent which, like *S. rhodanthum,* had n = 7. The close morphological resemblance between 11- and 18-chromosome strains of *S. rosea* points to a closer relation between them than the first alternative suggests. To support the idea that the ancestral chromosome number in Rhodiola is 6, it is significant that Baldwin (1937) suggested for Section Telephium, the most closely related section of *Sedum* cytologically known, an ancestral number of 12, or possibly 6.

In polyploid or hyperploid plants, some bivalent chromosomes at metaphase I of meiosis often appear to be associated in groups of two or more. These "secondary associations" have been thought to be an indication of homology between all or parts of the bivalents involved, and perhaps to be manifestations of some sort of residual synaptic attraction. Cells exhibiting the maximum number of secondary associations and the minimum number of groups of chromosomes have been claimed to provide an indication of the ancestral chromosome number for a species or group of species.

Soeda (1944) attempted to determine the ancestral basic number for *S. rosea* var. *elongatum* by counting and tabulating the numbers and kinds of secondary associations observed in 65 sporocytes. The maximum number of secondary associations, observed in three cells, consisted of three groups of 3 bivalents plus one association of 2 bivalents. On this basis he suggested that the 11-chromosome strain of *S. rosea* might be a secondarily balanced hexaploid whose ultimate ancestors had only 4 chromosomes, and that the chromosomes of the gametic complement could be designated $A_1A_2A_3$ $B_1B_2B_3C_1C_2C_3D_1D_2$. He had also studied species belonging to other sections of *Sedum,* and he thought that these also gave evidence for a basic number of 4 in the genus. Baldwin (1940), following a study of still other species of *Sedum,* also concluded that 4 was an important ancestral number in the Crassulaceae. For reasons to be discussed in more detail elsewhere the present author thinks it very unlikely that this is true, either for *S. rosea,* for *Sedum,* or for the family.

Great caution should be exercised in drawing conclusions about ancestral chromosome numbers on the basis of evidence from secondary associations. This is particularly true in situations other than eupolyploidy. The interpretation of secondary associations in many cases is too much a matter of individual opinion, for there are no objective standards to dictate how close together bivalents must lie to form a secondary association. Also, there is no proof that secondary association indicates common ancestry for all or most parts of the bivalents involved, nor that homology is the sole cause of their proximity.

Attempts to tabulate secondary associations in the present material were soon abandoned. Bivalents seemed to exhibit all degrees of proximity, with no place to make a distinction between those which

might safely be called secondary associations and those which were more likely to be mere chance proximities. Levan's figures (1933) show no secondary association. Perhaps true secondary pairing occurs in this material, but study of it has no promise as a means of indicating ancient chromosome homologies here. It has often been observed that fixation can cause chromosomes to clump or group together, and this may explain some configurations that have been called secondary associations. Stebbins (1950, p. 362) also has concluded that secondary association is "not a reliable index of the exact basic haploid number possessed by the original ancestors of a group."

In view of these limitations on applying data concerning secondary associations, and since the maximum association was observed in only three cells out of 65, Soeda's suggestion that 4 is the ancestral number in *S. rosea* is not accepted here. It seems more likely the ultimate ancestors of the species had 6 chromosomes, but evidence from the many Asiatic species of Section Rhodiola will be necessary before this is much more than speculation.

It is interesting to consider the relation between the distributions of the two chromosomal strains of *S. rosea* and the glacial history of North America. The 11-chromosome strain is widespread in Eurasia, where it is the only one yet found. But in North America its distribution appears more limited, and thus far it is known only from the northeastern part. Since the latter area was almost entirely covered by ice during the Pleistocene, it must have been invaded by the species in Post-Pleistocene time. And since 11-chromosome *S. rosea* of northeastern America apparently cannot be distinguished either cytologically or morphologically from *S. rosea* of Europe, it clearly is more closely related to the latter than to 18-chromosome *S. rosea* farther west. Though many boreal species of northeastern America are considered to have come from the west (cf. Hultén, 1937), in the present state of evidence it seems more likely that 11-chromosome *S. rosea* reached the area from Europe. Fernald (1931) pointed to the many species in common between regions of northeastern America and northern Europe recently freed from ice as evidence for free interchange of floras until geologically recent times, and this strain of *S. rosea* appears to be a case in point. The possibility that it reached North America even since the last recession of the Pleistocene glaciers should not be completely ignored. Though its method of dispersal is not known, in attaining its present wide distribution on Arctic islands, the species in post-glacial time appears to have crossed water gaps fully as great as any between Europe and North America.

On the other hand, the 18-chromosome strain appears to be more widely distributed in North America, and in central California and New Mexico it occurs far beyond the limit of Pleistocene continental glaciation. Thus it may be an older resident. If so, the 11-chromosome strain can hardly have contributed to its origin, at least on this continent. The area of closest approach between the two chromosomal strains in northwestern America or northeastern Asia needs to be established. Hultén (1937) stated that *S. rosea* has no large gaps in distribution in the Old World, "but a large one in the Arctic American Archipelago between northern Labrador and Alaska." It is likely that this gap separates the 11-chromosome strain on the east from the 18-chromosome strain on the west. However, study of more populations of the species from western North America, and especially Alaska, to determine whether the 11-chromosome strain is represented there at all is highly desirable.

A particularly critical population lives, or once lived, atop Roan Mountain, on the North Carolina-Tennessee state line (*"Rhodiola roanensis* Britton"). Sev-

eral attempts to obtain cytological material from this locality have been unsuccessful, and it now seems the colony is nearly or quite extinct. This is most unfortunate. If the hypothesis that the 18-chromosome strain has been on this continent longer is correct, it would be predicted that this population probably belonged to that strain, representing a remnant surviving in a glacial refuge area. The two 18-chromosome populations in New York could then be northward migrants from this area. On the other hand, they might represent an invasion from western sources.

Summary

Chromosomes of *Sedum rosea*, a circumboreal species, from 15 localities in North America were studied. Seven populations, all in the northeast, have $n = 11$ or $2n = 22$, as do populations previously reported from six localities in the Old World from Greenland to Japan. At eight localities in the United States, the species has $n = 18$ or $2n = 36$. Though the species is highly polymorphic, little or none of its morphological variation appears correlated with the difference in chromosome number. No sex chromosomes were identified; nor was it possible to classify secondary associations. The only other American species of Section Rhodiola, *S. rhodanthum*, and its Chinese relative *S. dumulosum* both have $n = 7$.

It is suggested that the 18-chromosome strain may have arisen either as an amphiploid, with the 11-chromosome strain as one parent, or as a hexaploid with respect to a basic number of six in the section. Evidence from distribution, however, suggests the 11-chromosome strain is of more recent arrival in North America, probably coming from Europe, and possibly even since the last glaciation.

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GEOGRAPHIC VARIATION IN THE NORWEGIAN SEA-URCHINS, *STRONGYLOCENTROTUS DROEBACHIENSIS* AND *S. PALLIDUS*

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INTRODUCTION

The study of natural species among marine invertebrates has lagged far behind similar work among the higher terrestrial animals. In particular, little work has so far been done on geographical variation, and even less on isolating mechanisms. The present studies were undertaken to contribute observations on these subjects.

In a previous paper (Vasseur, 1951) concerning *Strongylocentrotus droebachiensis* and *S. pallidus* of Tromsö it was shown that these species are differentiated from each other in respect to a number of characters. It was stated that some of these differentiating characters varied considerably along the coast of Norway from Tromsö in the north, over Trondheim to Dröbak in the south. The sea-urchins at Tromsö and also at Trondheim were classified easily into *S. droebachiensis* and *S. pallidus*. However, at Dröbak the two species were so similar in appearance (habitus), that there was some difficulty in classifying the material, at least with help of only the habitus. This similarity in appearance in part of their range certainly accounts for the fact that many authors have considered them merely variants of a single species. In order to overcome this difficulty in classification with help of only the habitus, each individual at Dröbak was subjected to a more thorough inspection under the microscope, since especially the pedicellariae were found to be good systematic characters. Furthermore, the sperm agglutination test with egg-water (see below) turned out to be of invaluable help for the proper classification of "difficult" specimens.

This difference in ease of classification depended on a geographic variation of several different characters for both species, but usually more so for *S. pallidus* than for *S. droebachiensis*. In the following some of these variable characters will be dealt with in some detail.

MATERIALS AND METHODS

The sea-urchins were collected mainly at three widely different localities along the coast of Norway, at Dröbak in the Oslo fjord, at Trondheim, and at Tromsö. The studies were started at Tromsö in 1948 (April to July, the sea-urchins comprising the 1948 material being dredged in May and June) and continued first at Dröbak in 1950 (February–March) and finally, in 1951, at Trondheim (January–February) and at Tromsö (February–March).

In addition to these sea-urchins from Norway a small number of *S. droebachiensis* were obtained on the west coast of Sweden in 1951 during a visit to the Kristineberg Zoological Station at Fiskebäckskil. They were dredged off Hjeltö in the Kolje fjord.

The dredgings at Tromsö were carried out mainly off the south west coast of Tromsöya at the Telegrafbukta, all sea-urchins in the 1948 material and most of the 1951 material being dredged at this place; a few specimens of the 1951 material were dredged off Tromsöysund.

The majority of the material from Trondheim was dredged just outside the Biological Station, off Heggdalen, and only a few from off Leangen-Ranheim. This latter locality is interesting for the unusual population of almost pigment-free *S. droebachiensis* (Vasseur, 1951).

The sea-urchins from Dröbak were dredged at three localities in the nearest vicinity of the Biological Station: just outside the Station, at Småskjaer, and in Klosund, between Bergholmen and Håöya.

The sea-urchins at Tromsö and at Trondheim are easily classified into the two groups *S. droebachiensis* and *S. pallidus* by their difference in habitus. *S. droebachiensis* is colored very dark purple with long spines more or less at random, whereas *S. pallidus* is light red or whitish green with short spines which are arranged in distinct rows. The color of the spines is different too. The two species are thus so different in appearance at these two localities that the task of classifying the different individuals is an easy one.

Most specimens were, however, also studied under the microscope. This was done (1) to ascertain that the classification with only the habitus had been correct; (2) in order to learn the differences in the microscopic characters with absolute certainty. In this way the correctness of the classification of the Dröbak material, where the difference in habitus was not so obvious in some cases, was improved. There remain, however, in this Dröbak material a few doubtful specimens, since my experience in the proper classification had not attained the rather high degree of proficiency which I obtained during the recent visits to Trondheim and Tromsö.

Most of the distinguishing microscopical characters (see below), as well as the macroscopical ones, have been recognized by G. O. Sars (1871), who was the first to describe *S. pallidus*. The difference in the shape and size of the globiferous pedicellariae (not described by Sars) proved, however, to be the most useful morphological character for classifying more doubtful specimens.

After the external characters had been studied on the living specimens the sea-urchins were opened by a circular cut in the soft tissue of the peristome around the lantern, the lantern was lifted out, the body fluid emptied and the body cavity rinsed two or three times with sea-water. Then the gonads were carefully loosened, lifted out with forceps, and placed in small bowls for the sperm-agglutination test (see below). By this method of opening, the test was kept undamaged and therefore could be used afterwards for studying several morphological characters statistically, e.g., number of pore-pairs per arc and size of lantern. Unfortunately, in order to take out the gonads many of the sea-urchins of the Dröbak material were cut by the usual circular cut along the ambitus before the above-mentioned method was discovered. These tests of course became damaged and could only be used for studying the arrangement of the oculars.

The undamaged tests were further treated in the following way. The viscera were removed, and the lantern put back into the test together with a piece of paper with the number of the particular specimen. Then the test was fixed for some time in 2 per cent formaldehyde in sea-water and thereafter transferred to two lots of 95 per cent alcohol and then dried. Finally, the dry test was brushed free from spines, tube-feet, etc.

Discussion of Some Characters

1. *Color of test.* Adult live specimens of *S. droebachiensis* are colored dark purple, whereas those of *S. pallidus* are red to whitish green. This pigmentation varies to some extent with the size of the animal and also with the latitude of the habitat.

Small specimens of *S. droebachiensis* are so light in their coloration that they could be mistaken for *S. pallidus*. However, the latter are still lighter when young, with the pigment arranged in ten radial stripes, whereas in young *S. droebachiensis* specimens the pigment is arranged in five radial stripes. Furthermore, these small specimens are most easily classified by means of their globiferous pedicellariae (see below).

On the average, the specimens of *S. droebachiensis* of Dröbak are not as dark as those from Tromsö and Trondheim. The specimens from the Swedish west coast are still less pigmented. In fact, at these southern localities the radial arrangement of the pigment usually is evident, even in adult specimens. The adult specimens from Trondheim and especially from Tromsö are so strongly pigmented that they appear homogeneously blackish purple.

The coloration of *S. pallidus* goes in the reverse direction, the specimens of Dröbak being more pigmented than those of Tromsö. This means that the difference in pigmentation between the two species is increased on going north. This depends partly on the fact that *S. pallidus* does not attain a very big size in Dröbak, the large specimens of Tromsö —which were bigger than the largest *S. droebachiensis* in my material—being particularly pale (see Vasseur, 1951). This seems to be a very essential reason why *S. pallidus* from Lofoten-Bodö was recognized by G. O. Sars (1871) as a new species but denied as a true species by those who compared *S. droebachiensis* and *S. pallidus* from more southern localities. Diakonov (1933), in his treatment of the echinoderms of the Arctic seas, divides the species *S. droebachiensis* into *f. pallida* and *f. atroviolacea* on account of their very prominent color difference. His *f. pallida* is identical with *S. pallidus* and his *f. atroviolacea* with *S. droebachiensis*.

2. *Color and structure of spines.* The primary spines of *S. droebachiensis* from the Scandinavian seas are in most cases colored a lightish purple, specimens with green primary spines being less frequent (see also Jackson, 1912, p. 137). The secondary spines, however, are green in most specimens.

The spines of *S. pallidus* usually are brown, sometimes with more or less green mixed with the brown. At Dröbak, there were quite a few *S. pallidus* specimens with beautiful bluish purple spines, the pigment being accumulated particularly in the upper part of the spines.

The spines of *S. droebachiensis* are longer and have more wedges (about 24) than those of *S. pallidus* (possessing about 18). The grooves between the wedges appear to be much deeper in *S. pallidus*.

3. *Ocular plates.* The arrangement of the genital and ocular plates around the periproct is different in the various sea-urchin species, e.g., in the genera *Echinus* and *Psammechinus* the oculars usually do not reach the periproct, they are all exsert, whereas in the family *Strongylocentrotidae* usually one or two oculars are insert. Jackson (1912), in his phylogeny of the Echini, made a very thorough study on the arrangement of the oculars of most regular sea-urchin species and he worked out in particular detail the development and variation of the oculars in *S. droebachiensis* (p. 129–143).

Jackson's results are included in table 1 in a condensed form. The values for his eight localities along the east coast of the United States are combined in this table, since the variation shown at these places is rather slight in spite of the differences in salinity (see below). Between 88 and 97 per cent have oculars I and V insert; 0.5 to 10 per cent have only ocular I insert; and 0.5 to 3.8 per cent have oculars I, IV and V insert.

The Norwegian material is characterized by high variability. This is substantiated also by the unusually high number of specimens with an aberrant arrangement of the ocular plates (see table 1).

Jackson is of the opinion that the variation in the arrangement of the oculars for the most part depends on differences in the salinity of the sea-water at the particular locality. Therefore, a low salinity should show the least number of oculars insert, as for example in the "Gullmar fjord" (most probably Jackson's specimens come from the nearby Kolje-Kalvö-fjord system, see below), whereas under open ocean conditions with a high sa-

linity the percentage of three or more oculars inserted becomes high, as for example at Iceland and the Faroes (see table 1).

If this assumption is correct then the salinity of the Tromsö locality ought to be high, that of Trondheim lower and finally that of Dröbak the lowest. In fact, the salinity of Dröbak should then be the lowest of all the localities studied both by Jackson and the present author, since the percentage of only ocular I insert (39 per cent for *S. droebachiensis* and 46 per cent for *S. pallidus*) is by far the highest at Dröbak.

This is at least partly true, since the locality in Tromsö is remote from freshwater. The Heggdalen locality in the Trondheim fjord most probably has a low salinity owing to the nearby outflow of the Nidelv. The Leangen-Ranheim locality, on the other hand, probably is not influenced by the outflow of the Nidelv; the 12 specimens of *S. droebachiensis* which were obtained at this locality all have oculars I and V insert, which is a further confirmation that Jackson's interpretation might be correct, even though the material is by far too small.

Dröbak is situated in the inner part of the Oslo fjord. Professor Björn Föyn kindly informs me that the salinity at the habitat of these sea-urchins at Dröbak shows high fluctuations, from less than 25 per mille to 35 per mille.

In the vicinity of the Kristineberg Zoological Station *S. droebachiensis* occurs particularly in the Kolje-Kalvö-fjord system. Here the sea-urchins live at a depth of about 14–15 meters, where the water from a cold-water basin with high salinity, low temperature, and low oxygen

TABLE 1. *Variation of ocular plate arrangement in* S. droebachiensis *and* S. pallidus

Locality	Reference	All exsert	I insert	II insert	IV insert	V insert	I, II insert	I, IV insert	I, V insert	II, V insert	IV, V insert	I, II, IV insert	I, II, V insert	I, IV, V insert	II, IV, V insert	III, IV, V insert	I, II, IV, V insert	I, III, IV, V insert	Number of specimens
		Strongylocentrotus droebachiensis																	
Friday Harbor, Puget Sound, Washington	Jackson		11						1,149		2		6	31			1		1,200
East coast of U.S.A. 8 localities	Jackson	1	699	1	1	10	20	64	24,214	31	29	1	166	491	2		7	1	25,738
St. Pierre, Newfoundland	Jackson		12					1	178				2	1					194
Labrador	Jackson		5			1		3	175				1	15					200
Iceland and Faroes	Jackson		4					1	21				2	7					35
Tromsö, Norway	This paper		7						247				4	53			3		314
Trondheim, Norway	This paper	1	34		1		1	1	126			1	2	24		1			192
Dröbak, Norway	This paper		43		2		3		57				2	2					109
"Gullmar fjord," Sweden	Jackson		15				1	1	29				4						50
Kristineberg, Sweden	This paper		5						24				3	2					34
		Strongylocentrotus pallidus																	
Tromsö, Norway	This paper	1	15			1	1	1	234	1		1	10	34			3		302
Trondheim, Norway	This paper		44						73		1		2	8					128
Dröbak, Norway	This paper	1	65				1	1	67		2		2	2					141

content meets the surface water which is rich in oxygen and shows high variation in salinity and temperature (Borei and Wernstedt, 1934).

There is another conclusion which might be drawn from these figures and the interpretation of Jackson. The difference between the two species in this character is rather small, although on the whole certainly significant. *S. pallidus* is more abundant at deeper localities than *S. droebachiensis,* which as a rule is genuinely littoral (cf. Sars, 1871; Bidenkap, 1897), and since the salinity is higher at greater depths, the difference between the two species in reality is increased still more. At Tromsö, for example, owing to their relative abundance at different depths, most specimens of *S. pallidus* were dredged at a depth of 20–25 meters, whereas *S. droebachiensis* was collected mainly at about 10 meters.

4. *Pedicellariae.* It has been stated above that the globiferous pedicellariae offer the best possibility for distinguishing the two species from each other by purely morphological means. This would indicate that they do not vary to any more appreciable extent. However, I have not been able to perform sufficiently elaborate studies concerning their form and size to give a definite statement. But, on the other hand, my impression is that there is a rather slight variability in this character, at least along the coast of Norway. Much of the same argument holds good for the tridentate pedicellariae too, but here a greater variability seems to exist.

As stated in the earlier paper, *S. droebachiensis* has big globiferous pedicellariae which are longish ovoid in form and strongly pigmented with dark purple pigment especially in specimens of more than about 2 centimeters diameter. *S. pallidus* has small globiferous pedicellariae which are spherical and pigmented, particularly along the edges of the jaws, with the red pigment typical of this species.

When small specimens are compared under the dissecting microscope, the difference in size is especially obvious (see Vasseur, 1951, table 2). One might say that the globiferous pedicellariae of *S. droebachiensis,* as viewed under the microscope, look like red gooseberries (they are not so pronouncedly longish ovoid in small specimens, but more compact) and those of *S. pallidus* like red currants, both in size, form and color.

The tridentate pedicellariae of *S. droebachiensis* are slender and more or less pigmented. Their valves, which are elongated and compressed, touch each other in the closed condition over nearly their full length. The tridentates of *S. pallidus,* on the other hand, are robust in shape and quite prominent, since they are white and located particularly on the upper half of the test (Sars, 1871). Their valves, which are rather broad and leaf-shaped, diverge strongly and when closed touch each other only at the tips (cf. Diakonov, 1933).

5. *Number of pore-pairs.* According to G. O. Sars (1871) *S. pallidus* has six pairs of pores in each arc, whereas *S. droebachiensis* has five. His material came from Lofoten-Bodö, between Tromsö and Trondheim. He found that very occasionally specimens of *S. droebachiensis* had six pore-pairs in one or several arcs, but on the other hand he also found a few specimens of *S. pallidus* with as many as seven pore-pairs.

Figure 1 shows that on an average the number of pore-pairs in each arc is increased for both species on following the coast of Norway from south to north, but more so for *S. pallidus* than for *S. droebachiensis.*

Figure 1 is based upon average values from usually 90 arcs of pore-pairs for each specimen. The principle on which the counting of the arcs is based has been discussed in the earlier paper. It was attempted to count those arcs which were formed at the same age.

S. droebachiensis has a very pronounced frequency maximum at 5.0 pore-pairs per arc at Drōbak and also at

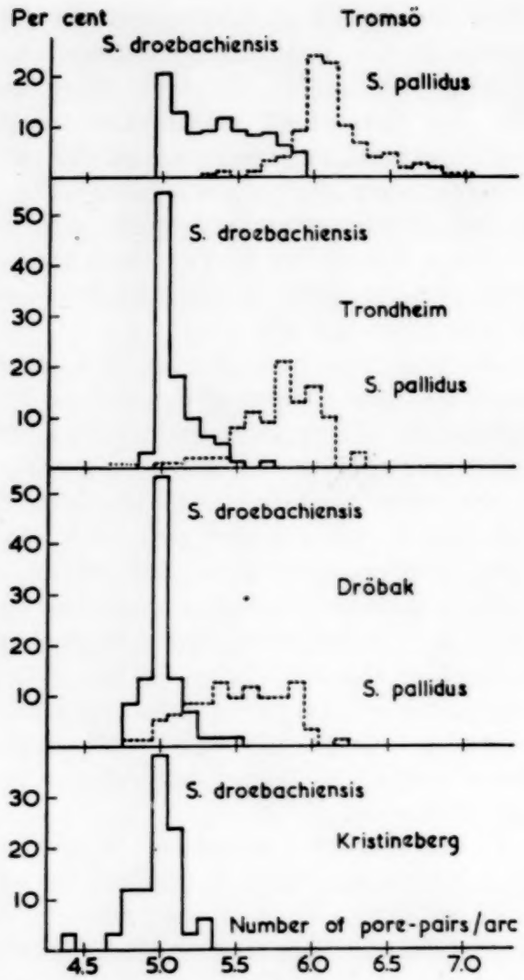

FIG. 1. Frequency distribution for the number of pore-pairs in each arc of *S. droebachiensis* and *S. pallidus*.

Trondheim, but this maximum is not very evident at Tromsö. At Dröbak (60 specimens) the values are distributed evenly around the maximum, whereas at Trondheim (167 specimens) they are unevenly displaced to the advantage of the higher values. This displacement is carried still further at Tromsö (206 specimens), where there are two maxima, one at 5.0 and one at about 5.4 pore-pairs per arc.

Finally, the diagram shows that at the west coast of Sweden ("Kristineberg," 34 specimens) the frequency maximum is situated at 5.0 pore-pairs per arc with the values slightly displaced to the low values.

The frequency maximum for *S. pallidus,* on the other hand, becomes more and more evident on going northward. At Dröbak (95 specimens) there is a broad maximum around 5.5 pore-pairs per arc. At Trondheim (100 specimens) the frequency maximum is more pronounced and has shifted to about 5.8. Finally, at Tromsö (150 specimens) the values are evenly distributed around the maximum, which is quite sharp and situated at about 6.05 pore-pairs per arc.

The histograms show that the two species are well differentiated in this character and statistical analysis gives very strong evidence that the difference is not due to chance. For example, the *t*-test for Dröbak, where the difference is least, gives $t = 13.37^{***}$, with $P < 0.001$.

This geographic variation in the number of pore-pairs receives additional interest by the finding of a similar variation in the irregular sea-urchin *Echinocardium cordatum*. This was discovered recently by J. B. S. Haldane (unpublished) in material collected at two localities off the coast of Brittany, France. He found the number of pore-pairs in the ambulacral areas Ia and Vb to differ significantly between the two localities Morgat and Locquémeau, whereas there was less difference for the other areas.

6. *Lantern.* At Tromsö the lantern of *S. pallidus* is, on an average, about twice as heavy as that of *S. droebachiensis* (fig. 2). However, the variability in size is very great in *S. pallidus*.

The most outstanding diifference is the very great difference in the growth rate for the lanterns of these species. In *S. droebachiensis* the growth curve has a logarithmic course throughout the life of the animal with but one value for k in Huxley's formula (1932) $y = b \cdot x^k$. In *S. pallidus* there is a much stronger increase of the weight of the lantern in the beginning. Then the growth rate decreases more or less rapidly for different specimens.

At Trondheim the lantern of *S. pallidus* is on an average smaller than at Tromsö, but it is still considerably larger

than that of *S. droebachiensis*. The variability in *S. pallidus* seems to be less than at Tromsö (see fig. 3).

At Dröbak, finally, the lantern of *S. pallidus* is still smaller and differs only very slightly from that of *S. droebachiensis* (fig. 4).

In *S. droebachensis,* on the other hand, geographic variation of this character is almost absent.

The material is insufficient for a more thorough statistical analysis. The lines are not true regression lines. Statistical methods were employed to construct these lines, but owing to the scantiness of the material these lines can only be considered as an attempt to summarize the values in a convenient way so that the differences in the growth rate will be more evident than is possible to bring forth by studying the individual values alone. The volume of the test has been calculated from the expression $D^2H/2$, where D = diameter, and H = height of the test. Even if this may not be absolutely correct, it may be considered as being equally valid for both species.

7. *Ecological differences. S. pallidus* prefers greater depths than *S. droebachiensis,* which as a rule is genuinely littoral (Sars, 1871; Storm, 1878; Bidenkap, 1897; Vasseur, 1951). Furthermore, at Dröbak most specimens of *S. pallidus* were dredged in Klosund, this locality containing an almost pure population of this species, whereas *S. droebachiensis* was the prevailing species at Småskjaer and outside the Biological Station. It would be of great interest to determine the ecological factors which differentiate these localities. Finally, *S. pallidus* has a tendency to cover itself with algae, shells, etc., which is not the case with *S. droebachiensis* (Vasseur, 1951).

8. *Spawning-season.* The spawning-season for *S. droebachiensis* is in early spring, usually in February to March, and presumably spawning occurs simultaneously at all three localities with perhaps a small difference in time. *S. pal-*

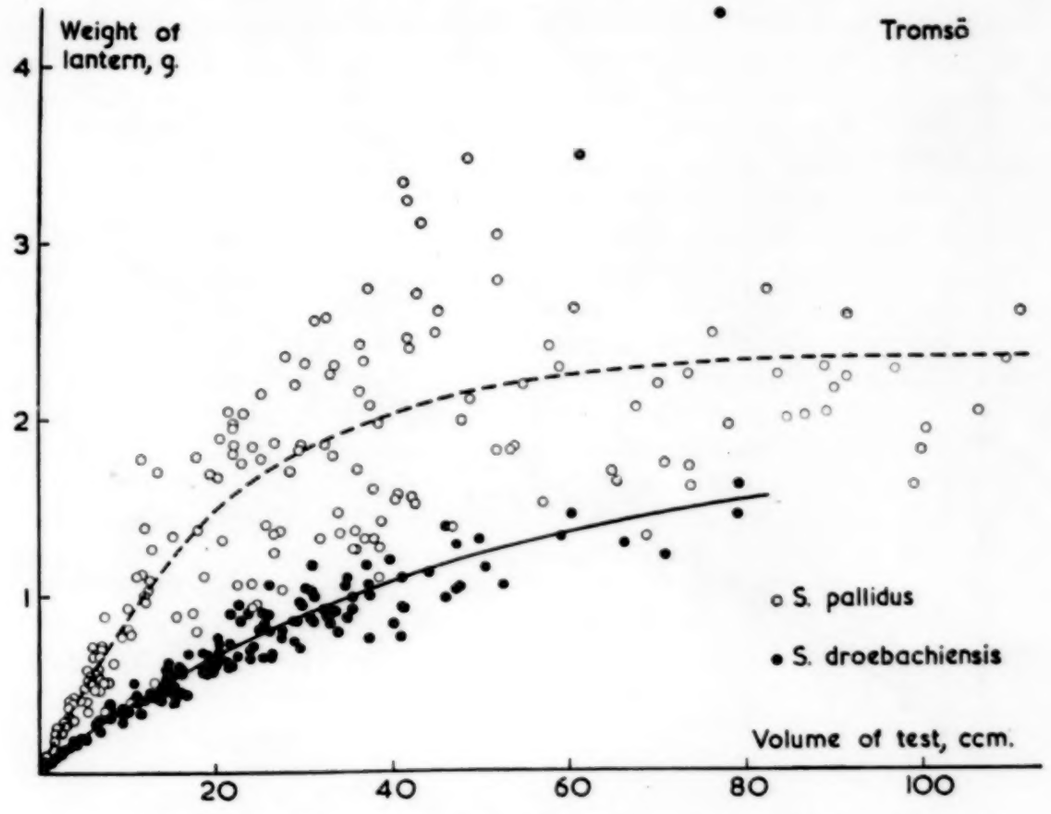

Fig. 2. Weight of lantern as compared with volume of test of *S. droebachiensis* and *S. pallidus* from Tromsö.

lidus, on the other hand, seems to show a greater variation. In Tromsö the spawning-season seems to be in June and July according to Kiaer's (1905) and my own observations (Vasseur, 1951). In the Kolski Bay of the Barents Sea Schorygin (1928) found mature specimens mainly in June.

The observations from Trondheim and Dröbak are even more scanty, but it seems as if *S. pallidus* at these places too spawns later than *S. droebachiensis*, though the chance for hybridization most probably is enhanced by an increasing overlapping period of the spawning-seasons on going south. However, since the two species show a certain difference in their ecological requirements, the risk of hybridization is diminished considerably. On the other hand this risk is not completely eliminated, as is shown by the presence of hybrids in the Trondheim material (see below).

9. *Sperm-agglutination.* The gonads were placed in small bowls, one bowl for each specimen. Each bowl was covered with a watch-glass to avoid evaporation. The testes with the sperm were placed in dry bowls. The ovaries with the eggs, on the other hand, were placed in bowls containing a few milliliters of sea-water. They were allowed to remain in contact with this at least for half an hour (at about 5° C.), before the supernatant sea-water ("egg-water"), which became charged with the sperm-agglutinating principle ("fertilizin"), was used for the sperm-agglutination test. Sea-water was not added to the testes until the particular sperm should be used for the agglutination test.

A few drops of egg-water were pipetted on a slide, which was placed on the stage of the microscope. A drop of a sperm suspension was then added and mixed with the egg-water by small circular movements. The course of the agglutination reaction was followed in the microscope and the strength of the agglutination noted.

As already stated above and more thoroughly discussed in the previous paper, the agglutination test could be used as a good auxiliary systematic character for

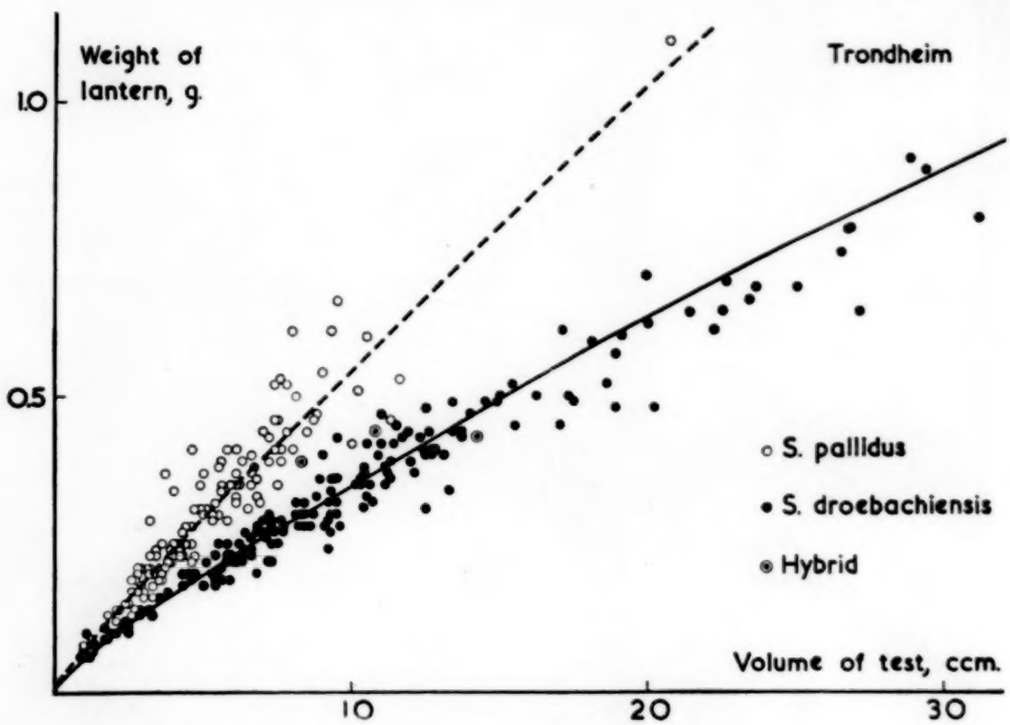

FIG. 3. Weight of lantern as compared with volume of test of *S. droebachiensis* and *S. pallidus* from Trondheim.

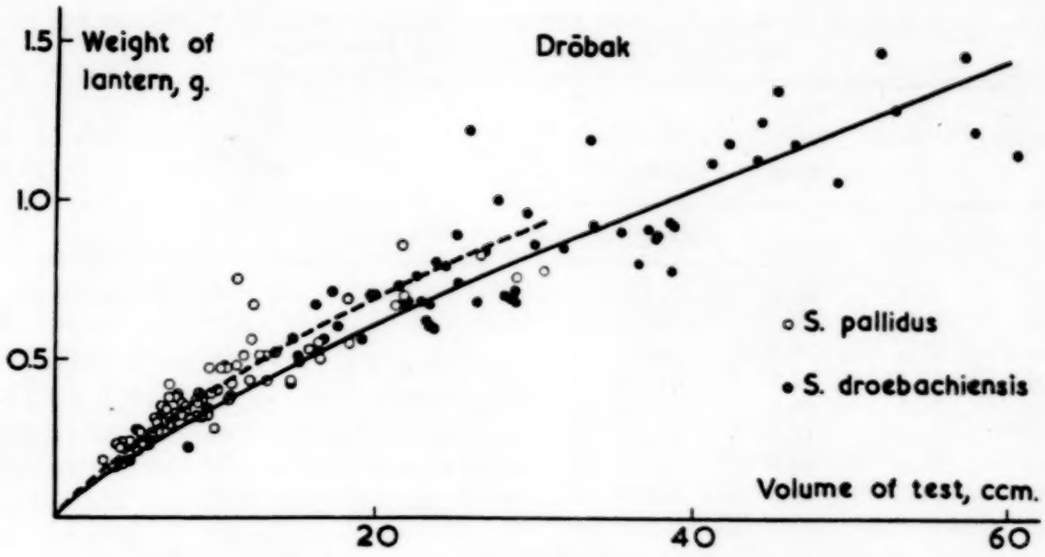

FIG. 4. Weight of lantern as compared with volume of test of *S. droebachiensis* and *S. pallidus* from Dröbak.

classifying doubtful specimens. In all, some five hundred individuals were tested as to their behavior to this test. The egg-water of *S. droebachiensis* was absolutely specific in all cases, giving agglutination only with *S. droebachiensis* sperm, whereas there were a few *S. pallidus* females the egg-water of which agglutinated also *S. droebachiensis* sperm. This agglutination was, however, not as strong as with *S. pallidus* sperm. This behavior of the egg-waters recalls the similar results obtained by F. R. Lillie (1921) with the Californian species *Strongylocentrotus franciscanus* and *S. purpuratus*.

In Trondheim three individuals (out of a total of 562 specimens) were found which according to their external characters were classified as hybrids (see table 2). Their sperm—all three were males—was agglutinated strongly by both kinds of egg-water, just as if they were both *S. pallidus* and *S. droebachiensis*. These individuals were the only hybrids in the whole Norwegian material (some 1,600 specimens). However, there is a possibility that there are one or two hybrids in the Dröbak material too (see below), even if this must be considered as very doubtful.

In addition to these hybrids two other males were found in Trondheim, the sperm of which gave agglutination with both kinds of egg-water although they were classified by their morphological characters as typical *S. pallidus* specimens. The cause of this abnormality is not understood at present, but further work on these problems is in progress.

There is indication of geographic variation in the strength of the agglutination reaction and in this case *S. droebachiensis* shows the higher variability, the agglutination being weakest in Tromsö (Vasseur, 1951, table 4). However, since the strength of the agglutination also depends on the maturity of the gametes, there is a possibility that some of this variability depended on the different degrees of maturity which were prevailing at the three stations when these tests were performed. No doubt seems to exist, however, that the intraspecific agglutination reaction is stronger in *S. pallidus* than in *S. droebachiensis*.

10. *Occurrence.* *S. droebachiensis* is known as a circumpolar species (Döderlein, 1905; v. Hofsten, 1915; Mortensen, 1943). It goes down to the southern part of the North Sea and is also found in Öresund (Brattström, 1941).

I have not been able to find *S. pallidus* in the Gullmar fjord or its surroundings,

TABLE 2. *Some data for the natural hybrids between* S. droebachiensis *and* S. pallidus *and for some specimens of the parent species at Trondheim*

A Specimen (nr.)	B Diameter (mm.)	C Height (mm.)	D Volume (ccm.)	E Weight of lantern (g.)	F $\frac{E}{D} \times 10^3$	G Pore-pairs per arc Mean value	H Ocular plates insert I	II	III	IV	V
Strongylocentrotus droebachiensis											
Td 31	39.8	20.4	16.157	.5041	3.12	5.30	+	−	−	−	+
45	39.1	19.5	14.906	.4893	3.28	5.00	+	−	−	−	+
126	37.9	19.5	14.005	.4749	3.39	5.01	+	−	−	−	+
100	37.4	17.9	12.519	.3145	2.51	4.99	+	−	−	−	+
68	34.9	18.1	11.223	.3661	3.26	4.96	+	−	−	−	+
95	34.0	18.3	10.577	.3482	3.30	5.08	+	−	−	−	+
177	31.6	16.9	8.438	.3223	3.82	5.00	+	−	−	−	+
191	31.3	16.8	8.229	.2771	3.36	5.03	+	−	−	−	−
Hybrids											
Td 148	38.2	19.4	14.156	.4330	3.06	5.69	+	−	−	−	+
105	34.9	17.7	10.779	.4427	4.11	5.48	+	−	−	−	+
165	32.5	15.8	8.344	.3851	4.61	5.42	+	−	−	−	+
Strongylocentrotus pallidus											
Tp 1	43.2	22.2	20.715	1.1028	5.33	5.98	+	−	−	−	+
83	35.5	16.6	10.460	.5950	5.69	5.84	+	−	−	−	+
117	34.6	17.0	10.176	.5121	5.04	5.80	+	−	−	−	+
112	33.4	16.6	9.259	.6091	6.58	5.82	+	−	−	−	−
23	33.1	16.0	8.765	.4720	5.39	5.83	+	−	−	+	+
107	32.3	16.2	8.451	.4410	5.22	5.66	+	−	−	−	+
20	30.8	17.0	8.063	.5042	6.24	5.89	+	−	−	−	+
41	30.4	16.4	7.578	.3932	5.19	5.62	+	−	−	−	−

but only *S. droebachiensis*. So at present, Dröbak is its southern limit. On the other hand, *S. pallidus* becomes more and more frequent as compared with *S. droebachiensis* at Finmark and in the Barents Sea, as is evident from the work of Schorygin (1928, p. 19). In fact, he reports (Schorygin, 1926) that the subspecies *atroviolaceus* Diakonov (i.e., *S. droebachiensis,* see above) is not found in the White Sea.

S. pallidus evidently is a more arctic species than *S. droebachiensis*. It has been reported from Lofoten-Bodö (Sars, 1871), the Trondheim fjord (Storm, 1878), the neighborhood of Tromsö (Bidenkap, 1897; Kiaer, 1905; Soot-Ryen, 1922), Barents Sea and the White Sea (Schorygin, 1926, 1928). More information of its occurrence seems to be lacking, since *S. pallidus* was not considered as a true species for more than some thirty years (Mortensen, 1903; Grieg, 1903; cf. also Bidenkap, 1897).

However, Jackson (1912, p. 137) mentions that a number of *S. droebachiensis* from St. Pierre, south of Newfoundland, "are of a light cream color, both tests and spines, giving them a very peculiar appearance. Specimens of a similar color occur also in material from Puget Sound, Washington." These may be *S. pallidus*. Furthermore, von Hofsten (1915, p. 135) discusses the variability of *S. droebachiensis* in the Icefjord of Spitsbergen and from this discussion it seems rather probable that *S. pallidus* is found there too.

Finally, the description given by Mortensen (1943) of *S. sachalinicus* Döderlein and particularly of *S. echinoides* A. Agassiz and H. L. Clark agree so well with *S. pallidus* that it appears quite pos-

sible that these three species in reality are one single species. This seems the more likely when the great geographical variation of *S. pallidus* along the coast of Norway is taken into consideration.

General Discussion

S. pallidus differs from *S. droebachiensis* in practically all the characters that have been studied. In those cases where a statistic evaluation of the characters has been possible, as for example the weight of the lantern and the number of pore-pairs, these characters show a more or less high degree of overlapping at the same locality.

Since *S. pallidus* differs from *S. droebachiensis* in having a larger lantern and more pore-pairs, it is of interest to see if the number of pore-pairs is in any way correlated with the weight of the lantern. One would expect that *S. pallidus* or *S. droebachiensis* individuals with an unusually high number of pore-pairs would also have an unusually large lantern, just as those with a low number of pore-pairs would have a small lantern. However, the correlation coefficients both for *S. droebachiensis* and for *S. pallidus* from Trondheim are practically zero as indicated by the regression lines (fig. 5). This shows that the individual variation in the weight of the lantern is completely independent of the variation in the number of pore-pairs in the two species at this locality. The lack of correlation between these two characters and the great variability in them indicates that both depend on more than one gene which are placed in different chromosomes and therefore show no or little linkage. Apparently, a set of plus and minus modifiers is involved in the mechanism.

That some of these modifiers may be linked is evident from an analysis of *S. pallidus* from Tromsö. In this material there is an unusually high variability in the weight of the lantern (see fig. 2).

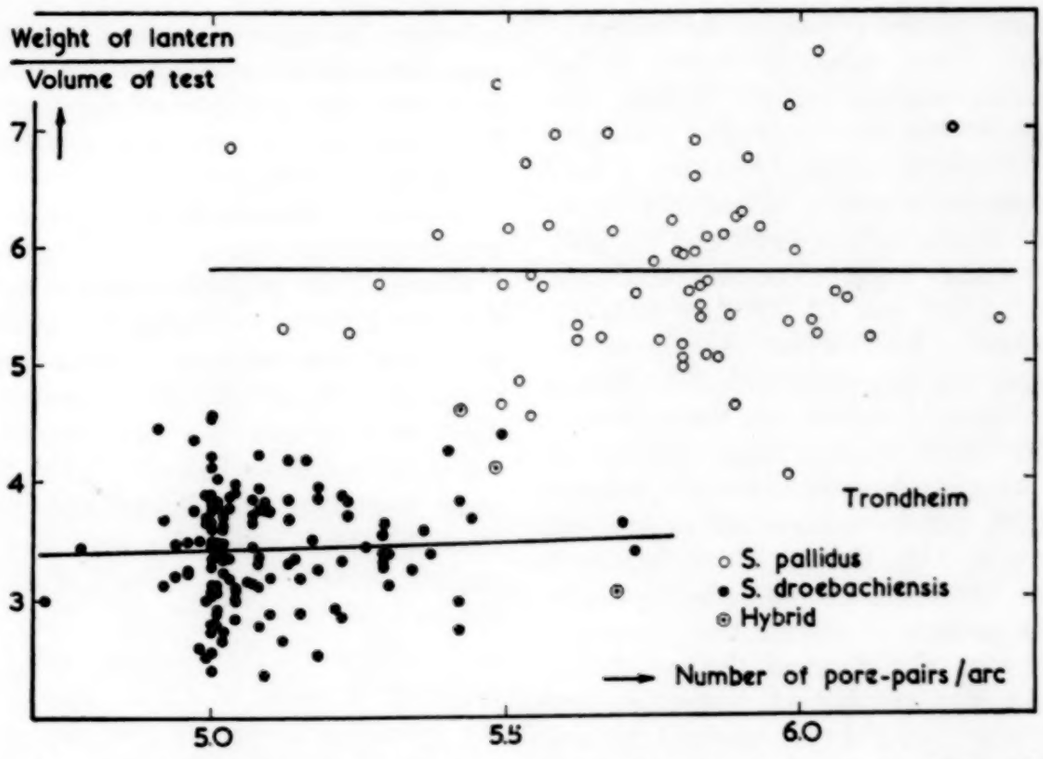

Fig. 5. Correlation between the number of pore-pairs in each arc and the relative size of the lantern, expressed by the ratio $\frac{\text{weight of lantern}}{\text{volume of test}}$, for *S. droebachiensis*, *S. pallidus*, and the natural hybrids between these species (Trondheim).

Specimens with a comparatively large lantern are very frequent, but specimens with a much smaller lantern—which however usually is decidedly larger than that of *S. droebachiensis*—are frequent too. Particularly the largest specimens have rather small lanterns. Specimens with a lantern of intermediate size between the two extremes are not so frequent, which indicates a special type of inheritance of this character (cf. Heuts, 1947). When the number of pore-pairs is plotted in the same way as in figure 1, both the specimens with a large and those with a small lantern show an even distribution of the values around the mean. However, the specimens with a large lantern show a mean value of 6.1088 ± 0.02763 ($n = 97$) pore-pairs per arc, whereas those with a small lantern have a mean value of 5.9983 ± 0.03147 ($n = 59$) pore-pairs per arc. The t-test gives $t = 2.64^{**}$, with $P < 0.01$.

The three hybrids from Trondheim (see table 2 and fig. 5) show a negative correlation between the number of pore-pairs and the ratio (weight of lantern)/volume. Their values lie exactly in between the centers for the highest frequency of the two species. However this negative correlation probably is only apparent, the material—three individuals—is of course far too small and the variability rather high. The two small hybrids, Td 105 and Td 165 (see table 2), are clearly intermediate in character. However the largest hybrid, Td 148, has a small lantern, falling into the area of *S. droebachiensis*, and a high number of pore-pairs, as is typical for *S. pallidus*. It might, therefore, be an offspring from specimens with strong minus modifiers for the lantern and strong plus modifiers for the number of pore-pairs.

For the calculation of the correlation between the number of pore-pairs and the ratio (weight of lantern)/volume (fig. 5) only the specimens with a volume of more than 5.0 cubic centimeters have been included, since the ratio is increased when the volume decreases. This increase is rather slight, down to a volume of about 5.0 cubic centimeters (i.e., a diameter of about 27 millimeters). For an absolutely correct interpretation this deviation ought to be taken into consideration. When this is not done in the diagram, the value for the difference which exists between the two species actually is decreased, since the values for the small *S. droebachiensis* specimens come into the area of the big *S. pallidus* specimens. In reality, therefore, the difference is still more pronounced.

There are in the Dröbak material several specimens which would have been difficult to classify with certainty without the sperm-agglutination test. This was particularly the case before I had discovered how useful the globiferous pedicellariae are in distinguishing these two species. But since the sperm-agglutination test failed in some cases, e.g., when the specimens were too small or had spawned already, there remained a few specimens which were uncertain in their classification. This should be expected, however, in materials where the difference between the species is rather slight and when the species are living partly in the same habitat and have overlapping spawning-seasons.

A similar difficulty in classification was encountered by Shearer, de Morgan, and Fuchs (1914) in their attempts to distinguish *Echinus esculentus* and *E. acutus* specimens from each other with absolute certainty. Here too the spawning-seasons overlap and the two species are found in the same habitat. They found some specimens which were more or less intermediate in character and they discussed whether these intermediate specimens were natural hybrids. They came to the conclusion that the intermediate appearance of some of these depended on the great variability of the two species and that they probably were not hybrids. One or two of these intermediates, however, were considered as being true hybrids.

According to several authors (Döderlein, 1905; v. Hofsten, 1915; Mortensen, 1943) the genus *Strongylocentrotus* originated from the North Parific. The species *S. droebachiensis*—and most probably *S. pallidus* too—from there spread all over the Arctic seas and then down into the North Atlantic. Whether or not this spreading occurred only in the eastward direction, as Döderlein (1905) thought, or in both east- and westward directions, as von Hofsten (1915) found more probable, is very difficult to ascertain.

The analyses of the arrangement of the oculars (see table 1) suggests that the two species have come to Norway from the east coast of North America, since the variability in this character is increased on going eastward. The data in table 1 indicate further that during this long wandering the genetic constitution has been altered, so that the influence by outer conditions is enhanced. It is rather unlikely that, e.g., the high percentage of only ocular I insert at Dröbak and on the west coast of Sweden depends on a salinity which in comparison with all East American localities and Trondheim is especially low.

The influence of genetical and environmental factors, as for example geographic latitude and salinity (cf. Heuts, 1947), on the different variable characters is quite obvious from these studies. But the data presented are not sufficient to decide which of the different factors are the more important. It seems probable that one character is modified more by one factor and another character more by another factor. This is demonstrated, for example, by the 12 specimens from Leangen-Ranheim of the Trondheim fjord. With the exception of their color and the arrangement of their oculars these 12 specimens do not show any deviation—as to the number of pore-pairs and the weight of the lantern, for instance—from the Heggdalen specimens. I hope to be able to obtain further information on these questions in the future.

Summary

The studies reported in this paper were carried out in Norway on the sea-urchins *Strongylocentrotus droebachiensis* and *S. pallidus* at Dröbak in the southern part, at Trondheim in the middle part, and at Tromsö in the northern part. A few data on material of *S. droebachiensis* from the west coast of Sweden are included too.

These two species can be differentiated from each other by a number of characters. The majority of these were recognized by G. O. Sars (1871) who was the first to describe *S. pallidus*.

Most of these characters show a pronounced geographic variation. This variation has been analyzed with statistical methods for the number of pore-pairs in each arc, the weight of the lantern, and the arrangement of the ocular plates. Furthermore, the color of the test shows a distinct geographic variation.

The best distinguishing characters, besides the habitus, are the globiferous pedicellariae and the sperm-agglutination test with egg-water.

At Trondheim three natural hybrids (out of a total of 562 specimens) were dredged. The data of these hybrids have been compared with those of normal *S. droebachiensis* and *S. pallidus* individuals from Trondheim.

Acknowledgments

I want to take the opportunity of thanking Professor J. B. S. Haldane for his permission to quote his unpublished figures on *Echinocardium cordatum*.

My sincere thanks are due to the directors and the staffs of the Biological Stations of Dröbak, Trondheim, and Kristineberg, and the Museum of Tromsö for working facilities and help with the dredgings, and to Mr. B. Hagström for help and discussions. Miss Hedvig Tamm and Mr. Walter Pudeck have assisted in the statistical work.

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RATES OF EVOLUTION IN THE COELACANTH AND DIPNOAN FISHES

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INTRODUCTION

The Crossopterygii and the Dipnoi are the only vertebrate orders known to span the long time interval between the Devonian Period and Recent times. Together they make up the subclass Choanichthyes, a group of fishes characterized by the presence of internal nostrils and many features of the skeleton setting them apart from the other major group of bony fishes, the Actinopterygii. Of the two suborders included in the Crossopterygii (Romer, 1945), the Rhipidistia became extinct in the early Permian, while the Coelacanthini have persisted to the present time. The rhipidistians, in spite of their relatively short history, are important, as they gave rise to the tetrapods as well as to the coelacanths. The dipnoans, or lungfishes, were derived either directly from primitive rhipidistians or from a common ancestral group that also gave rise to the rhipidistians.

The Coelacanthini were already well defined by the middle Devonian, the time of their first known appearance in the fossil record. They are found in strata of all subsequent geologic periods, except the Tertiary, when apparently they entered the open sea which provided little opportunity for preservation. The single Recent genus, *Latimeria,* is known from one specimen obtained in the coastal waters of South Africa.

In spite of the long history of the coelacanths, they have not been particularly successful in terms of the total number of described genera (about 27) or in terms of adaptive radiation. On the basis of known evidence, the peak of their diversification was reached in the Triassic, but for this period only 11 genera have been reported and, with a few exceptions, the various morphological specializations in these are of rather minor significance. The Devonian coelacanths, with one probable exception, have been found in marine formations, suggesting a marine origin or, more likely, an early marine radiation. There is only negative evidence for supposing that the coelacanths as a group deserted the marine environment by the Mississippian. It is possible that they have inhabited the seas since their origin, with a few fresh-water invasions. The known Carboniferous and Permian coelacanths occur in fresh-water sediments, while the Triassic genera are about 60 per cent marine. The other Mesozoic genera and, of course, *Latimeria* are marine.

The dipnoans are an equally well differentiated group, with the first known representative occurring in marine rocks of early Devonian age. This genus (*Dipnorhynchus*) retained a high percentage of primitive rhipidistian characters, and it is probable that the lungfishes arose in the early Devonian. Although the total number of genera is about the same as in the Coelacanthini, the greatest number (15) for any one geologic period is recorded from the Devonian, suggesting that the maximum radiation occurred early in the history of the group. The Devonian genera are found in fresh-water, brackish, and marine formations (Romer and Grove, 1935; Westoll, 1949), and there was a short-lived marine invasion at this time if not a marine origin for the group. In later geologic periods the dipnoans are found almost exclusively in fresh-water deposits, and the three living genera are also fresh-water inhabitants. Occasional post-Devonian

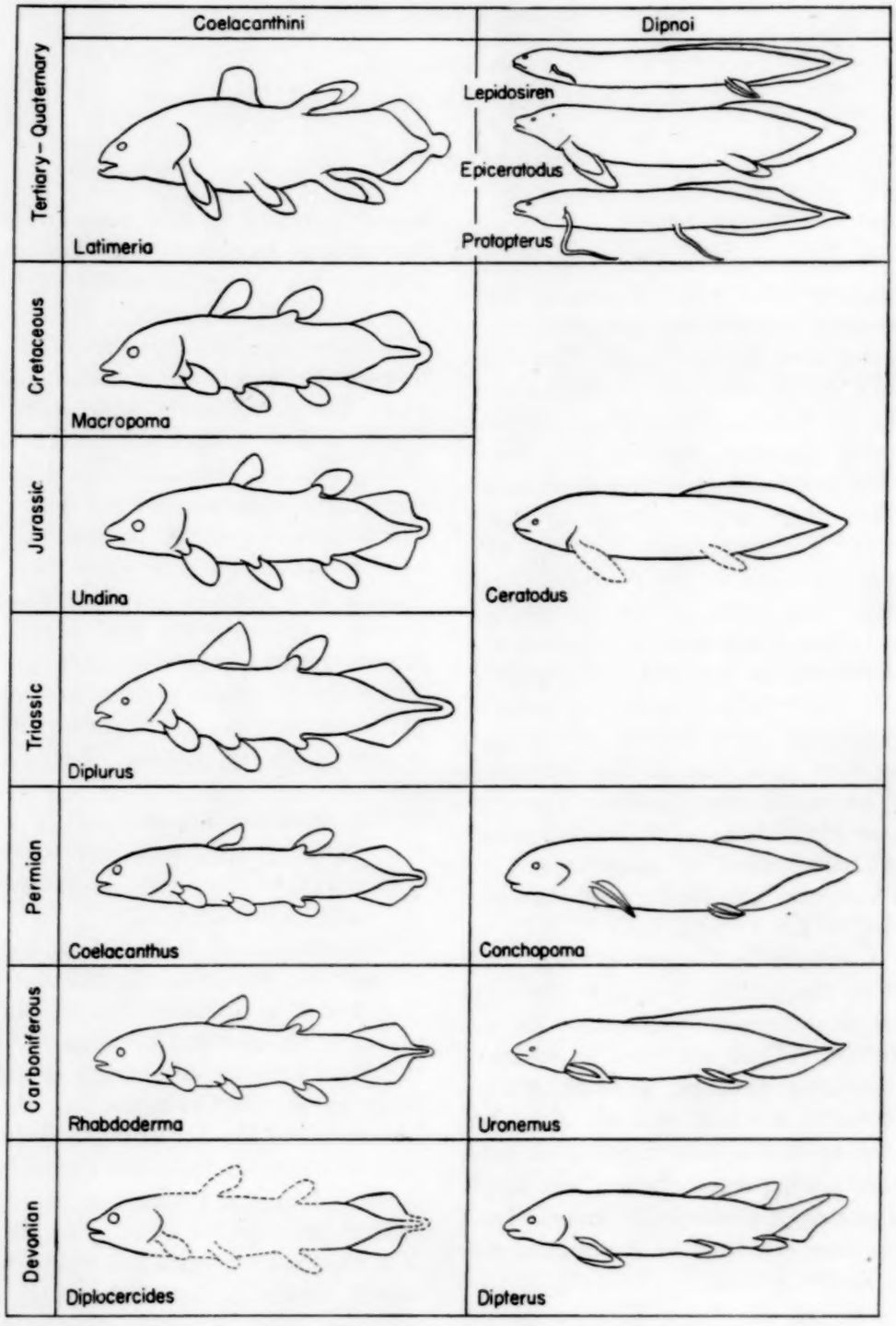

FIG. 1. Representative coelacanth and dipnoan genera for each of the geologic periods in which these groups occur. *Diplocercides* after Stensiö; *Coelacanthus* after Moy-Thomas and Westoll; *Latimeria* after Smith; *Dipterus* after Traquair; *Uronemus* after Traquair; *Conchopoma* after Weitzel; *Ceratodus* after Wade. *Latimeria* is unknown in the Tertiary. The outline of *Ceratodus* is based on *C. formosus* from the Triassic of Australia, the only species of this Mesozoic genus in which the body is well preserved.

remains occurring in brackish-water or marine sediments almost certainly represent animals carried into these environments after death.

Although the relationships of the Coelacanthini and Dipnoi are now rather well understood, and their systematic positions more or less settled, the subdivision of each group into families remains arbitrary since it has not been possible to determine with any degree of certainty the phylogenetic relationships of the included genera (see, for instance, Olson, 1951). It is possible, however, to arrange a series of contemporary or geologically successive genera that do not necessarily have an ancestor-descendant relationship, but that demonstrate the major evolutionary trends.

Within both the coelacanths and dipnoans, a few genera show rather striking divergent adaptive modifications in the skeleton. The time required for the origin of these specializations is unknown, but in terms of the total history of these fishes it is evident that these modifications were of relatively short duration. It will be obvious from what follows that they cannot be considered in determining an evolutionary rate for the entire group based exclusively on morphologic data, although the genera possessing them must be utilized for any rate employing taxonomic units.

The purpose of this paper is to consider the nature and validity of two sorts of evolutionary rates that may be determined on the basis of the long fossil record of the Coelacanthini and Dipnoi. The factual data have been obtained from various sources. Those for the coelacanths were compiled for a recently completed paper by the writer (in press) and those for the dipnoans have been taken mainly from Westoll (1949).

Morphologic Rates

There are, in general, two sorts of evolutionary rates that may be determined by the paleontologist—morphologic rates and taxonomic rates (Simpson, 1944; 1949a and b). The temporal morphologic rates, as opposed to intra- or inter-group relative morphologic rates, are most frequently computed on the basis of time units in years rather than on strata thickness, which cannot be accurately correlated with absolute time, or on geologic epochs or periods which have varying durations.

Temporal morphologic rates are best expressed in quantitative terms, usually by changing the morphologic measurements into some appropriate form, such as percentages, logarithms, or standard deviations, and by plotting these data against time. The usual method of computing such rates is in terms of single characters and their change per unit of absolute time. Such analysis is possible when the fossil record for a group of organisms is fairly complete, when evolutionary lines can be determined, and when the character selected is subject to reasonably accurate measurement in most or all members of the phyletic sequence. It is not always possible, however, to obtain accurate or meaningful measurements from a series of fossil specimens, and this is especially true of fossil fishes which are usually flattened, distorted, and often dissociated. Furthermore, most fish phylogenies are incomplete and arbitrary, being little more, as stated above, than morphologic series.

In view of these difficulties, it would appear that more significant results may be obtained if morphologic change in the entire organism is evaluated with a method that does not involve direct measurement. Simpson (1949, p. 207) has pointed out that consideration of morphologic rate in terms of the entire organism is not practical as "the whole organism involves too many separate characters for ready analysis and combination, and the more practical study of this broader aspect of evolutionary rate is by taxonomic methods." The taxonomic rate that reflects change in the entire organism, on a basis equivalent to a total sum-

mation of morphologic change, involves the use of genera as the best available estimates or expressions of the total change. Fossil genera are generally more clearly defined and relatively less subjective than fossil species. For a succession of genera that existed during a given time interval and that have a presumed ancestor-descendant relationship, the rate of evolution may be expressed in terms of average genera per million years for this interval (Simpson, 1944, p. 15 ff.). This is essentially a rate of total structural change in terms of genera.

In the absence of a sequence of successive, related genera (such as exists for the horses and perhaps for the camels, oreodonts, and a few other groups among the mammals) in many or most categories of lower vertebrates, it becomes necessary to devise another method for obtaining an absolute temporal morphological rate. A procedure developed by Westoll (1949) in a study of dipnoan evolution offers new possibilities in this direction.

For distinctive groups of fishes, such as the coelacanths and dipnoans, that have undergone little adaptive radiation and that include relatively few genera, there is an excellent opportunity to recognize a number of skeletal specializations that are present at the time the group first appears in the fossil record, or that develop subsequently and apparently involve all later genera. For convenience of morphologic analysis, the skeleton may be divided in the conventional manner into various character complexes such as braincase, skull-roof, cheek area, palate, vertebral column, girdles, etc. Although it would be highly desirabe to separate the skeleton more completely into functional units, this is not feasible in the present state of knowledge.

Westoll's analysis of dipnoan evolution is based on consideration of changes in twenty-one different skeletal and scale characters or relationships (i.e., bone fusions and eliminations). For each, he worked out a sequence of evolutionary, structural grades extending in time from the presumed ancestral condition to a later stage of morphological stabilization —which might be in the living genera or earlier in dipnoan history, depending on the character. To each of these grades he assigned a number, the most specialized condition being represented by zero, preceded by three to six progressively higher numbers. Each genus in the morphologic series was given one of these numerical ratings for each character or relationship. The morphologic ratings for each genus were then totaled to express the retention of primitive characters for a given genus. The presumed early Devonian ancestor received an arbitrary rating of 100 and the descendant genera progressively lower values with the Recent *Protopterus* and *Lepidosiren* retaining zero primitive characters. As might be expected, the values determined for nearly contemporaneous genera are slightly different, reflecting minor differences in evolutionary rate.

Westoll then plotted the generic totals against time to show graphically the loss of ancestral characters, but not the rate of loss per unit of time. By subtracting the rating for retained ancestral characters in each genus from the ancestral rating of 100, numerical values may be computed expressing the acquisition of advanced characters. These data can then be transformed into figures demonstrating the acquisition of advanced characters per million years for the approximate time interval between successive genera in the series.

For the coelacanths, thirteen character complexes were selected (Schaeffer, in press),[1] and the observable morphologic changes in each were listed by geologic periods. From this list the number of long-range, suprageneric morphologic advances present in a series of geologically successive genera was determined. Vari-

[1] These are: endocranium, palate, dermal bones of snout, skull-roof, cheek area, mandible, hyoid and gill arches, dentition, axial skeleton, paired fins and girdles, unpaired fins, squamation and dermal bone structure, and body form.

ous specializations, known to be of only generic significance, were not included. Morphologic rates were then determined, based on the number of long-range structural changes per million years for the time interval between the first appearance of two successive genera, or for a period including the ranges of several genera that show the same definable, long-continued modification.

By tracing the history of the various character complexes in the coelacanths and dipnoans, it is possible to determine roughly the time of appearance of each character advance or, conversely, the time when ancestral characters are lost. The rate of appearance of definitive coelacanth or dipnoan characters thus represents the total number of such characters present in a particular genus, divided by the time interval (in millions of years) separating the first appearance of that genus from a preceding, more primitive one in the morphologiical series.

This method of determining a morphologic rate is open to several criticisms which, however, do not necessarily invalidate the results. The analysis of the structural change is to some extent subjective and arbitrary. The manner in which the changes are counted makes it necessary to consider them of equal significance, although certain ones are undoubtedly interrelated, or are more important functionally and morphologically than others. The number of changes in a progressive coelacanth or dipnoan direction recorded in any one genus will be differently evaluated by different students, but it is believed that the relative number of advances for the entire series of genera will be nearly the same if the analysis is carried out in an essentially similar manner. The time interval between the first appearances of genera can only be roughly approximated, and variation in this determination will influence the rate and to some extent the shape of the rate curve. In spite of these difficulties, the *pattern* of the rate curves must represent essentially a true picture of the rate of addition or modification of long-range coelacanth and dipnoan characters.

The curves for the two groups (fig. 2) under consideration have essentially the same pattern in spite of the somewhat different methods employed in determining them. For both, the rate rose rapidly during the Devonian, representing the initial period of differentiation from the ancestral stock. This transitional period

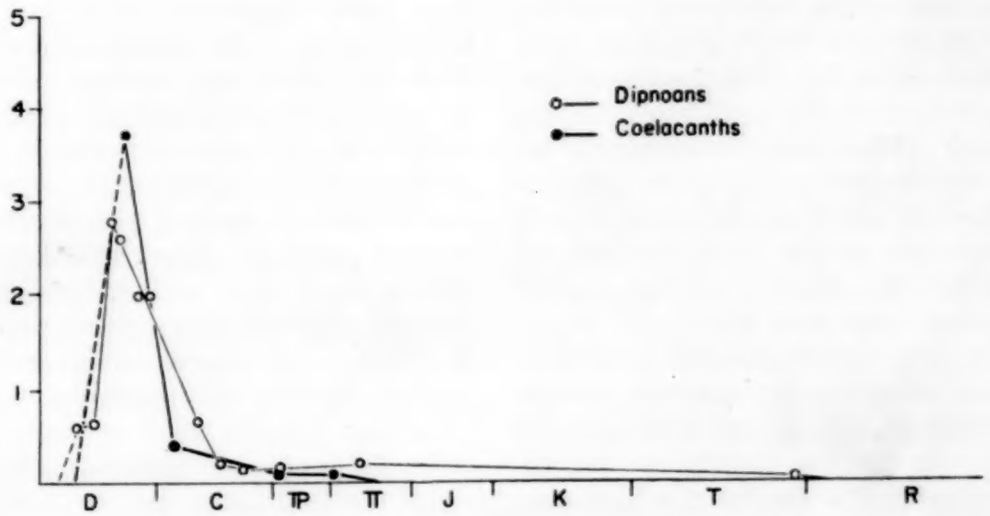

FIG. 2. Graph showing the rate of acquisition and subsequent modification of suprageneric morphologic characters in the coelacanths and dipnoans. The ordinate scale represents the number of character changes per million years. The Mississippian and Pennsylvanian periods are grouped here in the Carboniferous.

is apparently partly documented for the dipnoans by a single genus (*Dipnorhynchus*) which, although regarded as a dipnoan (Westoll, 1949), has retained many primitive characters (grading of 85 to 96 out of ancestral rating of 100 in Westoll's tabulations). An unnamed late Devonian coelacanth mentioned by the same author (1943) has rhipidistian-like paired fins, but it probably occurs too late in the record to be regarded as a true transitional type.

Although the duration of the transitional period cannot be exactly determined for either group, there is good reason to believe that the ancestral stocks from which they arose were themselves not present before the early Devonian. The primitive rhipidistian crossopterygians, which gave rise to the coelacanths and possibly to the dipnoans, are represented in the late early Devonian by a single rare genus (*Porolepis*). The late Devonian coelacanths have a very rhipidistian-like braincase and the unnamed form mentioned above still retained rhipidistian-like paired-fins. Aside from indicating differential rates of evolution in the skeleton, these facts suggest a not-too-remote origin from the rhipidistians. A reasonable estimate for the length of the interval between the beginning of coelacanth trend and the first known appearance of this group is about 14 million years, which is somewhat less than one-third of the total length of the Devonian. The term "transitional period" has various evolutionary implications, but in terms of the fossil record only, it refers to the rarely documented interval between the initiation of a particular trend from some known or postulated ancestral stock and the time when the first recognizable members of the descendant group appear in the fossil record.

The accelerated rate at the beginning of coelacanth and dipnoan history (about 3.7 character modifications per million years for the coelacanths and 2.8 for the dipnoans represent the approximate maximum rates) existed during the transition period and it must be related to the successful occupation of ecological niches that were either unoccupied or vacated by less successful competitors. The particular selective factors associated with this morphological change are difficult to postulate on the basis of the inadequate fossil record. A rapid change is adaptive zones is, however, clearly indicated.

The rapid decrease in the morphological rate of both groups during the late Devonian and early Carboniferous may be correlated with the fixation of structural patterns that have persisted, with only minor modification, to the Recent. The various environments inhabited by the dipnoans and particularly the coelacanths since their first appearances in the fossil record indicate wide adaptive tolerances. There are no skeletal modifications above the generic level that can be definitely correlated with the differing selective forces that must have existed in the various environments inhabited by these fishes. As Westoll (1949, p. 174) has pointed out, the dipnoans developed a fin structure and body form indicating sluggish locomotion, together with changes in the skull and dentition that resulted in a highly specialized triturating bottom-feeding mechanism. The skull modifications were nearly completed in the late Devonian and the post-cranial changes were well under way at that time. The coelacanths likewise evolved a specialized skull and post-cranial skeleton by the middle or late Devonian. The skull, however, shows no marked general trend toward a particular type of feeding habit; genera are known with triturating, presumably plankton-feeding and predacious dentitions. The post-cranial skeleton is remarkably constant; its design indicates powerful, though not normally rapid, swimming and good maneuverability.

In the dipnoans, as emphasized by Westoll (*ibid.*, p. 176), the number of side branches from the main evolutionary line are relatively few and the structural modifications are not radical. The same

is true, in general, for the coelacanths. Intraspecific variability in the dipnoan dermal skull was high in the Devonian, apparently absent during the Carboniferous and Permian, and again high in the living genera (Westoll, 1949, p. 178). The degree of variation in the coelacanth dermal skull has not been examined with the same thoroughness, although this should be possible for a number of well represented genera. In the late Triassic genus *Diplurus* there is considerable variation in the dermal bone pattern of the anterior portion of the skull roof, while the remainder of the dermal skull is apparently very constant. The variations in the dermal skull pattern in the coelacanths, at either the intraspecific or generic levels, appear to have little functional significance and no long-range pattern trends can be observed. In the dipnoans there has been a trend toward reduction in the number of skull-roof bones, either because of fusion or elimination, and a tendency for them to sink deeply into the skin.

The available data provide scanty evidence for considering specific causes for the bradytelic (low-rate) portions of the rate curves, which represent over three-quarters of the time duration of each group. There is little basis for discussing any possible genetic mechanism; population size at any given time level is difficult to estimate; particular physical environments inhabited by members of the two groups may have been stable for long periods, but invasion of different environments did not appreciably alter the morphologic rate, at least in the skeleton (see below).

Selection pressure, in the form of competition provided by the contemporaneous and rapidly-evolving actinopterygian fishes, was undoubtedly present in most of the environments occupied by the coelacanths and dipnoans. It must have played an important role in limiting adaptive radiation by excluding a great variety of ecologic nitches.

Simpson (1944, p. 141) is of the opinion that a low evolutionary rate "results from the equilibrium of large breeding populations of animals specifically adapted to a continuously available environment that is relatively invariable or has a rhythmic variation that corresponds with adaptive tolerance in the population." The coelacanths and dipnoans rapidly became adapted to the environments available to them. For the former the adaptation was broad and plastic, for the latter relatively narrow and specific. The lungfishes have spent most of their existence in a fresh-water, bottom habitat, presumably feeding mainly on worms, crustaceans, molluscs and some aquatic plants, as do their modern representatives. The question of dipnoan population size has already been discussed by Westoll (1949, p. 180). Large numbers of specimens of several Devonian genera have been obtained from single localities, and it is a reasonable assumption that large breeding populations were present. For later genera, including the Recent, the record is too incomplete for a positive statement, although it may be assumed that the breeding populations have been large enough to reduce the possibility of random modification and, of course, extinction.

The broader adaptation of the Coelacanthini is implied in their ability to inhabit at various times ecologic niches in fresh-water swamps and lakes as well as in epicontinental seas and the ocean. At the specific or subspecific level, however, adaptation may have been, and probably was, narrow for each of these niches. The absence of the coelacanths today in all these environments but the ocean may well be the result of the actinopterygian radiation. They have been mostly agile, predaceous, open-water forms (see also Westoll, 1941, p. 56), able to compete successfully for long periods with similar sorts of early actinopterygians, but not with the more advanced types, except in some as yet unknown oceanic environment. There is evidence of large populations for a number of coelacanth genera,

but, in general, little more can be stated regarding this matter than has already been said for the dipnoans.

Since the coelacanths have apparently inhabited a greater variety of habitats than the dipnoans, it is perhaps reasonable to assume that the causes of bradytely are more complex in the former than in the latter. The morphological rates are based entirely on skeletal change; whether they would be appreciably different if the soft anatomy could be similarly evaluated is a moot question. It is entirely possible that the major changes in coelacanth habitat were accompanied by alterations in the respiratory mechanism and in the excretory system, but concerning these it probably will never be possible to obtain direct information. Nevertheless, the skeleton does provide a reasonably good index of vertebrate organization and reflects major changes in a number of other organ systems such as the muscular, nervous, and to some extent the circulatory and the respiratory systems.

The rapid acquisition of the ordinal and subordinal characters in the dipnoans and the coelacanths during the first part of their long history is undoubtedly also the case for other groups within the Osteichthyes. The earliest actinopterygians, the paleoniscoids, appear fully differentiated in the middle Devonian, having arisen from some unknown ancestral stock during the early Devonian or possibly the late Silurian. The characters shared in common by the more advanced subholosteans apparently required less than the total duration of the Permian for their development. The various holostean groups were differentiated rapidly in the Triassic and at least one group arose during the last part of the Permian. The main lines of the complex teleost radiation evolved at an accelerated rate during the early or late Cretaceous (depending on the line under consideration). The most primitive clupeoids were already differentiated by the early Jurassic and another clupeoid group, the elopids, apparently evolved during the late Jurassic. Most suborders and even families of teleosts for which there is any sort of an adequate fossil record were already well established at the beginning of the Tertiary. There is thus reason to believe that the morphologic rate curves for nearly all the higher categories of the Osteichthyes would be similar in general pattern to those for the coelacanths and dipnoans. Since the curves are meaningful only on a comparative basis, it would be highly desirable to determine morphologic rates for the other groups of fishes with adequate data.

Taxonomic Rates

Among the various types of taxonomic evolutionary rates that have been discussed by Simpson (1944, 1949a and b), the origination rate (number of new genera per million years) appears to be most applicable to the groups under consideration. Phyletic taxonomic rates cannot be employed, mainly because the detailed phylogenies of the coelacanths and dipnoans have not been worked out, and the durations of the various genera cannot be determined with any degree of accuracy. Rates of taxonomic diversification may be expressed by the time-frequency curve (discussed by Simpson, 1949, pp. 218–220), but this method cannot be utilized, again for the reasons just mentioned. In addition to these deficiencies, the subjectiveness of the taxonomic units must be considered. Most of the coelacanth and dipnoan genera utilized in the determination of the morphologic rate are accepted by paleoichthyologists as clearly distinctive. The remaining genera that also should be considered in the determination of a taxonomic rate are based on fragmentary or frequently very incomplete specimens, and some of these genera, particularly for the Devonian dipnoans, may be too inclusive, or be synonyms of other genera. The taxonomic allocation, however, is probably generally as objective as in most groups

of fossil vertebrates, and perhaps better than in many, because of the relatively few genera, most of which are well separated morphologically and temporally.

The interpretation of an origination rate has been considered by Simpson (1949a, p. 220; 1949b, p. 103). When a single, rapidly changing evolutionary sequence is involved, the origination rate is essentially one of structural change, or of change in the average characters of a series of populations. When any degree of radiation is involved from a central ancestral stock, the origination rate is mainly one of morphologic diversification. Thus, although these rates, in terms of new genera per million years, may be identical, they represent in their pure form quite different situations. In practice it is frequently impossible to distinguish between them, and in groups such as the coelacanths and dipnoans undoubtedly both sorts of origination rates were present at different times. Without any satisfactory information on phylogenetic relationships, it would be presumptuous to state that the origination rates for these groups for any given time level represent one or the other type. There is, however, concrete evidence of taxonomic diversification, and it may be suspected that the curves largely represent this phenomenon.

The origination rates for both the dipnoans and the coelacanths (fig. 3) remained consistently low throughout their long history. In spite of the deficiencies of the record, these rate curves extending over about 300 million years, must represent essentially the true picture. The relatively higher rate for the dipnoans during the late Paleozoic, in contrast to the coelacanth, may, in part, be the result of the fragmentary record and the present almost unavoidable taxonomic inflation. The increase in the coelacanth rate during the Triassic represents the greatest known radiation of this group, as previously noted by Zeuner (1946).

For comparison with the coelacanth and dipnoan curves, origination curves

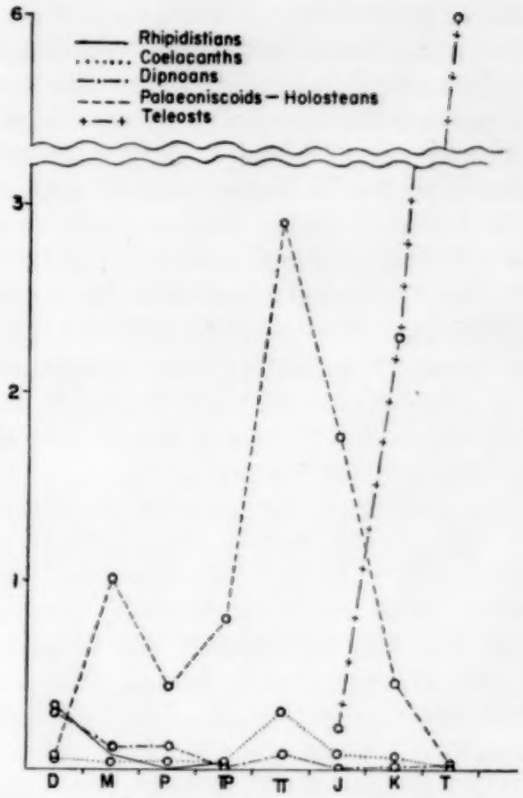

FIG. 3. Graph showing the origination rate of genera per million years for the coelacanths, the dipnoans, the palaeoniscoid-holostean complex, the rhipidistians, and the teleosts. The ordinate scale represents the number of new genera per million years.

for the rhipidistian crossopterygians, the paleoniscoid-subholostean-holostean complex and the teleosts have been determined. As can be noted by simple inspection of the rhipidistian record, the rate is highest in the Devonian and falls off rapidly to the Permian when the group became extinct. The minor drop in the Pennsylvanian is probably the result of a record deficiency. The contrast between the choanichthyid and actinopterygian rates is very striking. The paleoniscoids underwent rapid taxonomic diversification during the Mississippian, but suffered a decline in the Pennsylvanian when various subholostean and holostean lines were arising from different paleoniscoid stocks. The high point of the curve in the Triassic represents the subholostean radiation, which present evidence limits to this period, plus the holostean groups

existing at that time, some of which also arose from the subholosteans. Although the holosteans continued their radiation throughout the remainder of the Mesozoic, the rate declined rapidly from the Triassic to the Tertiary, where it reached a level that probably has remained constant throuhout the Cenozoic. The teleosts had an explosive radiation beginning in the Jurassic, possibly—but not certainly—from a single holostean stock. The origination curve for this vast assemblage is without doubt mainly one of taxonomic diversification.

Comparison of the origination curves for the choanichthyids and actinopterygians offers further indication that the former were unable to compete successfully with the evolutionary potentialities of the actinopterygian fishes, either in fresh water or in the sea. The holostean rate was reduced to the choanichthyid level by the rise of the teleosts, which undoubtedly have been able to fill not only many old holostean niches but many new ones as well.

The origination rate curves are based entirely on paleontological samples since it is practically impossible to apply the same sort of sampling factors and techniques to the Recent fish fauna. There were certainly many environments inhabited by fishes in the past that are rarely, if ever, represented in paleontological samples—torrential streams, coral reefs, and the deep sea, to mention a few. This rather obvious fact may be regarded as a serious objection to the validity of evolutionary rates, even though such rates can only be obtained by the use of fossil data. This criticism may be answered in several ways. Paleontological samples nearly always omit the sorts of environments just mentioned, and in this sense they are self-consistent. The paleontologist can work only with the data made available by intensive sampling of the represented environments. Furthermore, a rate representing evolutionary change through many millions of years, even if biased, must approximate the real one. The teleost origination curve, for instance, should probably be steeper, at least for the late Mesozoic and early Tertiary, but the exceedingly rapid origination rate is well demonstrated on the basis of the available data. As in the case of the morphological rates, the general curve patterns, on a comparative basis, have greater significance in evolutionary considerations than any single curve, or portion thereof.

The morphologic rate curves for the coelacanths and dipnoans are expressing the rate of structural change at the highest taxonomic level for each group. Only long-range modifications that affected the entire group are considered. The origination rates represent morphologic change or taxonomic divergence at the generic level. The former, therefore, represents the rate of evolution in the basic structural organization of the group, and the latter, the rate of intragroup diversification. Because they are based on different types of data, the morphologic and taxonomic rate curves cannot be directly compared. It is of interest, however, that they demonstrate a slow evolutionary rate for the coelacanths and dipnoans, both in fundamental morphology and in adaptive radiation. This correlation, which is perhaps to be expected in many bradytelic groups, is found in the lingulids (brachipods), in the sphenodontids among the reptiles, and in the didelphid marsupials among the mammals.

Summary

Although the coelacanth and dipnoan fishes have existed from the middle Devonian to the Recent, they have had a limited adaptive radiation and each group includes only about 27 known genera. The phylogenetic relationships of these genera has not been satisfactorily determined, and subdivision of the Coelacanthini and Dipnoi into families must be regarded as tentative. It is possible, however, to arrange a sequence of contemporaneous and geologically successive

genera in a morphologic series that demonstrates the principal suprageneric evolutionary trends.

A morphologic evolutionary rate curve has been determined for each group, based on the number of suprageneric structural changes per million years for the time interval between the Devonian initiation of the coelacanth or dipnoan trend and the Recent epoch. The rate increased rapidly during the early history of each group but declined during the late Devonian and early Carboniferous to a low level that remained almost constant to the Recent. The accelerated initial rates presumably were associated with a change in adaptive zones and with the successful occupation of various available ecologic niches. The decline and subsequent leveling of the rate curves may be related to the fixation of suprageneric structural patterns which, for the coelacanths, had rather broad adaptive tolerances and, for the dipnoans, rather narrow ones. Decreasingly successful competition with the rapidly evolving and radiating actinopterygian fishes was probably responsible for the early environmental restriction of the dipnoans and the later elimination of the coelacanths from fresh-water habitats.

Taxonomic evolutionary rates are based on the number of new coelacanth and dipnoan genera per million years. The resulting curves appear to demonstrate mainly rates of taxonomic rather than rates of morphologic diversification. The curves are generally low throughout the history of both groups, in contrast to similarly determined origination rate curves for the main categories of actinopterygian fishes. The actinopterygian curves undoubtedly reflect a far greater taxonomic dispersion, and this is certainly true for the nearly vertical teleost curve. Comparison of the origination curves for the choanichthyids and actinopterygians further indicates that the coelacanths and dipnoans were unable to compete successfully with actinopterygians.

The limitations of paleontological sampling have biased both sorts of evolutionary rate curves to some extent. Nevertheless, it is maintained that the curve patterns would not be greatly altered if samples representing the probable missing environments could be obtained. The morphologic rate curves indicate the tempo of structural change at the highest possible taxonomic level; the origination rate curves demonstrate morphologic and, to some extent, taxonomic divergence, at the generic level. Both sorts of rates show the bradytelic evolutionary pattern that persisted throughout most of the history of the coelacanths and dipnoans.

Acknowledgments

The writer is obligated to Drs. Karl Koopman, Norman D. Newell, and G. G. Simpson for critically reading the manuscript.

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NATURAL SELECTION IN THE LIZARD GENUS *ARISTELLIGER*

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INTRODUCTION

There are few who doubt that natural selection is one of the primary factors in evolution. Any study therefore that reveals to some degree the complex workings of selection must broaden our understanding of organic evolution itself. This paper attempts to contribute to the knowledge of selective forces in nature by reporting some observations on a small West Indian lizard of the genus *Aristelliger*.

In some ways the Squamata, the order of reptiles containing the lizards and snakes, present the ideal material for evolutionary study, for members of this order possess an epidermis divided into complex, genetically determined scale patterns. The discrete, meristic nature of the scale characters makes easy an objectivity in study which is difficult in dealing with such standard characteristics as body proportions or the variations of color tones in plumage and pelage. It is with a character in the scutellation of the lizard *Aristelliger* that this paper is concerned.

Phenomena indicating natural selection have often been demonstrated in the study of reptiles. Most of these demonstrations involve scale characters of snakes. Some examples are: Dunn (1915) on *Natrix sipedon,* Stuart (1941) on *Dryadophis boddaerti,* Inger (1942) on *Opheodrys vernalis,* Inger (1943) on *Thamnophis sirtalis,* Underwood (1944) on *Natrix piscator,* Klauber (1945) on *Crotalus viridis,* and Mertens (1947) on *Natrix natrix*. Dunn (1942) reviewed the subject of selection in the scutellation of snakes and pointed out the serious neglect of studies of natural selection by students of taxonomy. All of the above studies involve comparisons of the variations of the scutellation of the young and that of the adults, and show that the variation of the young exceeds that of the adults, while many of the juvenile scutellation patterns do not appear within the range of variation of the adults. This can best be interpreted as differential selection against the more aberrant phenotypes. None of the authors of these studies was able to demonstrate the functional significance of the characters or the selective mechanism operating. The present study attempts to show the adaptive significance of a scale character subject to differential selection, and thus, it is hoped, to go beyond the stage of mere inference.

THE GENUS *Aristelliger*

The genus *Aristelliger* belongs to the family Gekkonidae, the members of which occupy a rather special adaptive zone. Most of the species of this family are arboreal, although primitively terrestrial as well as secondarily terrestrial forms exist. There are no known burrowing, aquatic or herbivorous forms. A study of the morphology of this family reveals a rather stereotyped skull but a most varied toe structure, probably correlated with climbing habits. Because of the striking nature of the variation in toe structure the taxonomy of the geckos has been based largely on digital morphology. These lizards are primarily nocturnal, but some have become secondarily diurnal. The members of the family are endowed with vocal powers.

Aristelliger has typically gekkonid habits in being crepuscular, insectivorous and arboreal. But unlike many other geckos, which lay their eggs in clutches of two (Loveridge, 1947), *Aristelliger* lays a

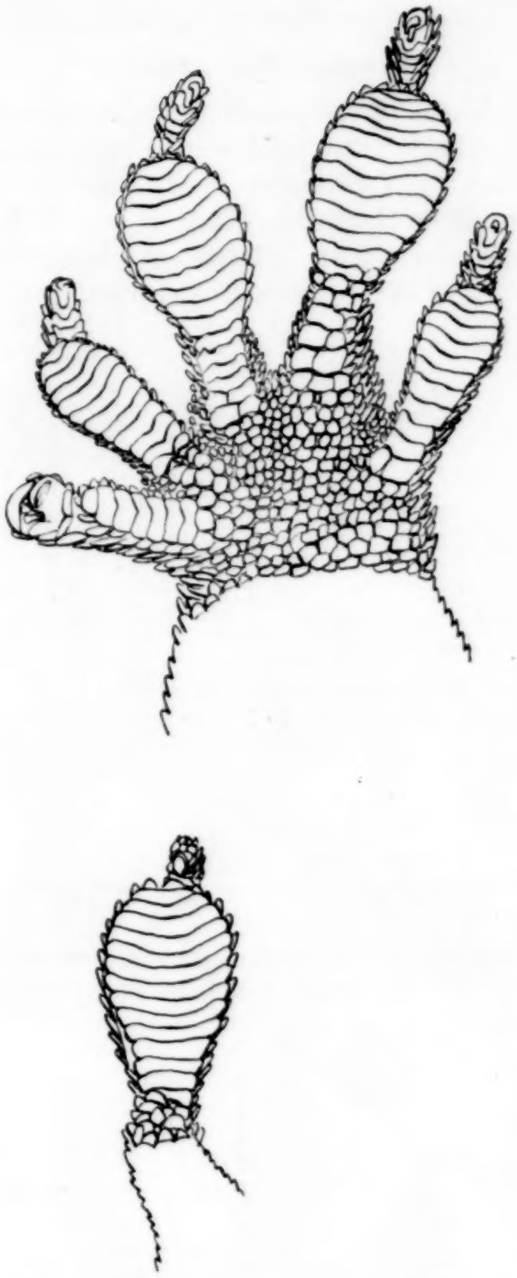

FIG. 1. Forefoot and fourth hind toe of *Aristelliger praesignis*, showing the lamellae of the ventral surface.

single egg in a clutch. These eggs are laid communally in holes in trees, hollow branches, and crevices in the bark, as often as twice a year. Approximately three months are required for incubation.

Aristelliger belongs to a large complex of genera with amphicoelous vertebrae. These genera are distributed over Africa, Eurasia, Australia, New Zealand, Oceania, and tropical America. *Aristelliger* can be distinguished from all other gekkonid genera by a peculiar terminal shield that surrounds the first claw of every foot (fig. 1). The genus resembles and may be related to genera (e.g., *Phyllopezus, Tarentola,* etc.) in which the claw arises from the middle of a swollen digital pad; the ventral surface of which bears a series of transverse lamellae (fig. 1).

Aristelliger may be divided into two subgenera, the primitive subgenus *Aristelliger,* and the more modified subgenus *Aristelligella.* The subgenus *Aristelliger* contains four living and one fossil species. They are: (1) *A. georgeensis* (Bocourt) of the coastal islands and Caribbean coast of Central America, (2) *A. praesignis* (Hallowell) of Jamaica, Swan, and Cayman Islands, (3) *A. lar* Cope of Hispaniola (4) a new species from the southern Bahamas (to be described elsewhere), (5) a fossil species, *A. titan* Hecht from Jamaica. The subgenus *Aristelligella* is monotypic and its single species, *A. cochranae* Grant, is composed of three subspecies on the islands of Navassa, Hispaniola and Great Inagua.

BREEDING AND MAXIMAL SIZE

There is a correlation between minimal breeding size and maximal size attained by the various forms in this genus (table 1). *Aristelliger cochranae barbouri* (Noble and Klingel) of Great Inagua has the smallest minimal breeding size and the

TABLE 1. *Minimal breeding and maximal sizes in* Aristelliger

Subspecies virtually identical with the nominate subspecies in the characters tabulated are not included in the table.

Form	Minimal breeding size	Maximal size
A. cochranae barbouri	35 mm.	50 mm.
A. cochranae cochranae	35 mm.	60 mm.
A. praesignis	45 mm.	85 mm.
A. georgeensis	85 mm.	115 mm.
A. lar	100 mm.	135 mm.
A. titan	——	Estimated 160 mm.

smallest maximal size in the genus, and *Aristelliger lar* Cope of Hispaniola has the largest minimal breeding size and the largest maximal size among living forms. As may be seen from table 1, *A. praesignis* is intermediate in both features. These facts indicate a close correlation between the attainment of reproductive maturity and size potential.

The Infradigital Lamellae

Structure and number

Lizards of the genus *Aristelliger* show remarkably little variation in most characters. An exception is the number of infradigital lamellae, which is one of the most important systematic characters, useful in the separation of species. As is

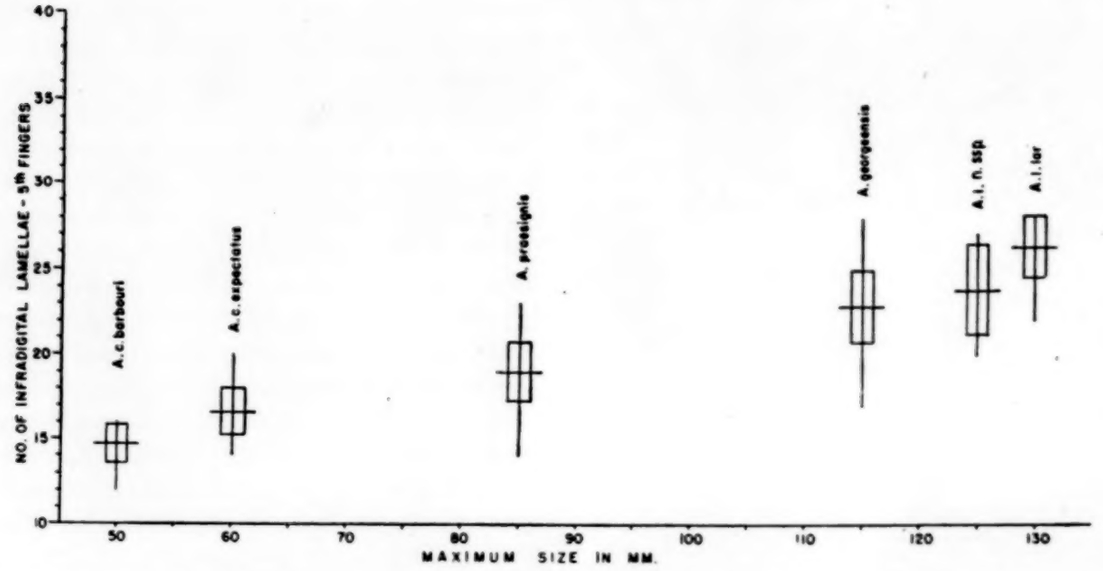

FIG. 2. Graph showing the correlation between maximum size of the forms and the number of infradigital lamellae on the fifth finger. Vertical line—the range; horizontal line—mean; rectangle—standard deviation.

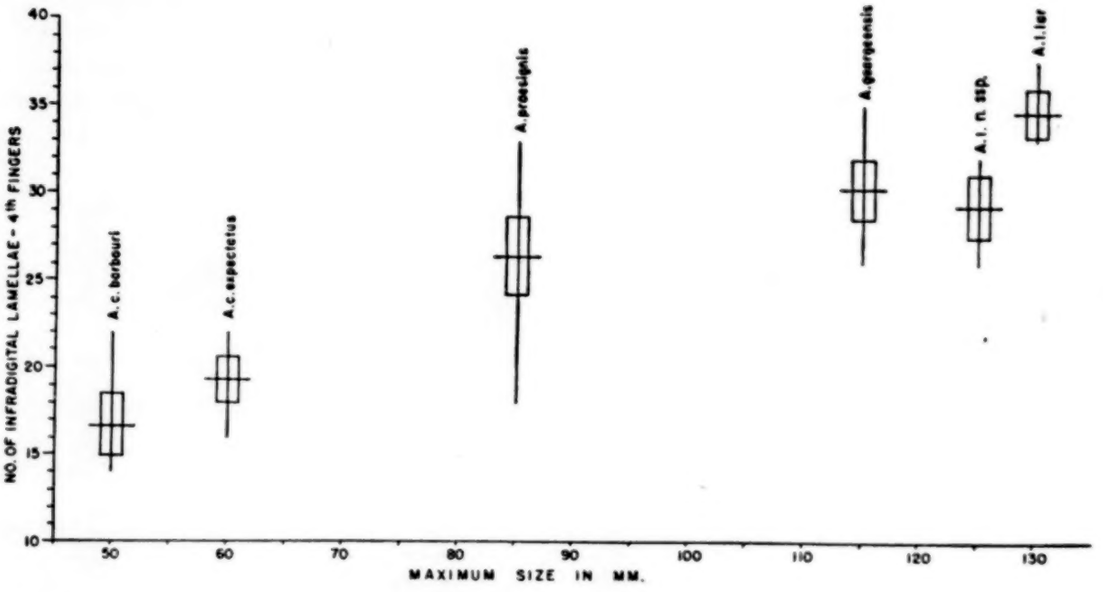

FIG. 3. Graph showing the correlation between maximum size of the forms and the number of infradigital lamellae on the fourth finger. Vertical line—the range; horizontal line—mean; rectangle—standard deviation.

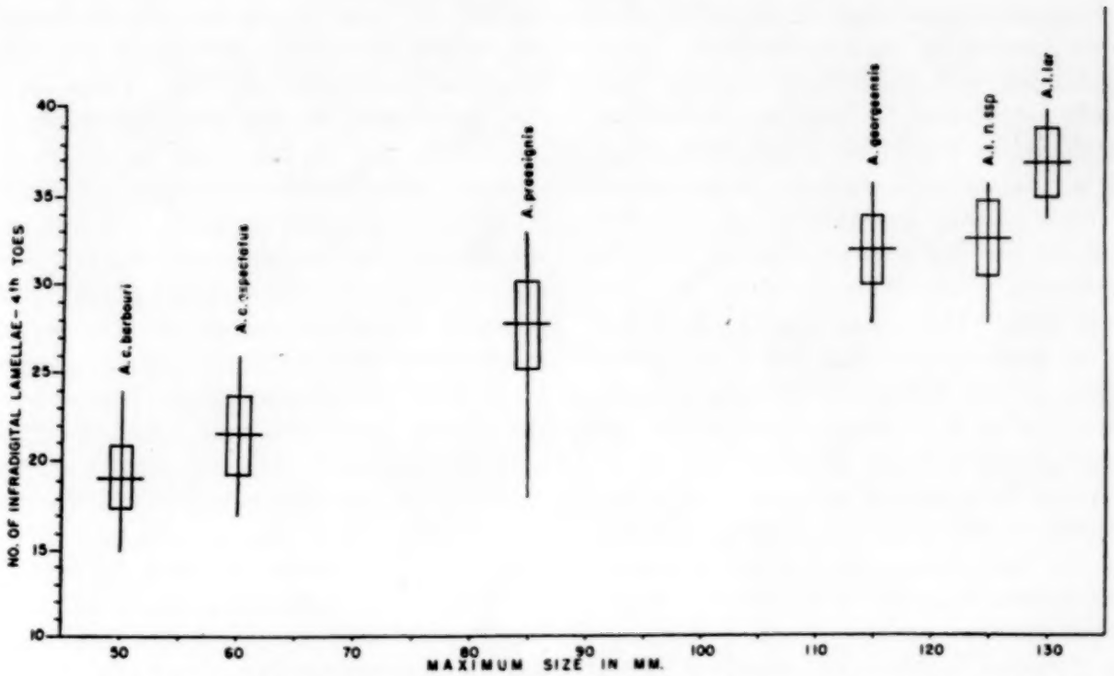

FIG. 4. Graph showing the correlation between maximum size of the forms and the number of infradigital lamellae on the fourth toe. Vertical line—the range; horizontal line—mean; rectangle—standard deviation.

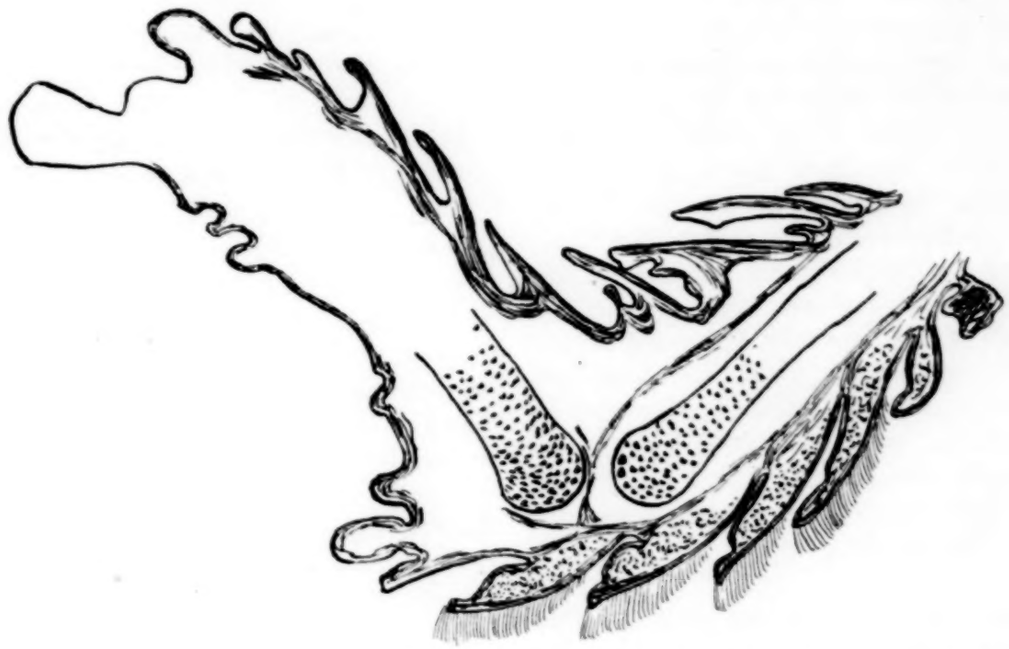

FIG. 5. Diagrammatic sagittal section of the fourth toe of *A. praesignis*. The microscopic hair-like structures are visible on the ventral surface of the lamellae.

shown in fig. 1, these are transverse plates arranged in a single linear series on the ventral surface of the toes. In the systematic study of the genus counts were made from the base to the anterior border of the dilated pad. A study of the lamellae of all the digits was made with particular emphasis on the fourth and fifth fingers and toes. Since there were some asymmetrical counts, it was necessary to add the number of lamellae on the corresponding right and left finger or toe in order

to present the number of lamellae as a single number for each individual. Thus, a specimen with 10 lamellae on the right fourth finger and 11 lamellae on the left fourth finger would be presented as having a total of 21 lamellae. Since asymmetrical counts are infrequent, the frequencies for the odd number of lamellae are always lower than those for the even numbered. The most useful characters for this study are the lamellae of the fourth finger and toe, which are the largest digits and probably bear the greatest weight and strain as the animals climb or run about.

As can be observed in figures 3–5 a correlation exists between lamellae number and the maximum size for each species. The lowest number of lamellae is found in the smallest species, *A. cochranae,* and the greatest number of lamellae in the largest species, *A. lar.* A similar correlation occurs between subspecies of the same species such as *A. c. barbouri* and *A. c. expectatus.* The positive correlation between maximal size and the number of lamellae suggests that the number of the latter might be controlled by natural selection. Analysis of the length of lamellae indicates that there is a constant ratio of lamellar length to snout-vent or toe length in the entire genus. This ratio indicates that there is an optimal length of a lamella in a given region of the toe pad that is mechanically necessary to afford the maximum flexibility with the maximum gripping surface. Perhaps if the lamellae were relatively longer the toe would lose its flexibility, and if the plates were shorter the toe might not afford the maximum gripping surface.

The function of the infradigital lamellae

The fact that these lamellae are located on the ventral surface of the digital pad indicates that they are involved in locomotion. Dellit (1934, 1949) and Mahendra (1940), in experiments on several gekkonid genera, have shown that the lamellae are involved in traction, particularly when climbing on vertical surfaces. They found small hair-like structures on the ventral surfaces of the infradigital lamellae, which structures are about .01 mm. long and have recurved tips. These hair-like structures on the infradigital lamellae, which may be compared to the cleats of a football player's shoes, give the lizard an efficient gripping surface. It was observed that the lizards were able to climb on dirty glass, but not on clean glass. Presumably these structures aid the lizard in climbing on vertical surfaces in nature. Even dead animals and those from which the claws were removed could cling to vertical surfaces. During shedding, the skin on the lamellae being cast with that of the body, there was a reduction in the ability of the lizards to cling to vertical surfaces. An examination made by Garth Underwood and myself of sections of the foot of *Aristelliger praesignis* (fig. 5) has revealed the presence of similar hair-like structures on the ventral surface of the lamellae. Observations made by the author on live *Aristelliger* show that, like other gekkonid genera, it has reduced climbing ability during shedding.

Intraspecific variation in the number of infradigital lamellae

This study is based on an extensive series represented by the subspecies, *Aristelliger p. praesignis.* The original analysis of the number of infradigital lamellae showed that there were small differences between geographic samples of *A. p. praesignis.* The samples showing these quantitative differences proved to consist of different size-groups. Upon reanalysis, after breaking down the material in different size classes, it was found that there are no statistically significant differences in lamellar number when samples of the same size group are compared. It was therefore possible to lump samples within the size classes from different localities so as to present a generalized picture. It may be observed (fig. 6) in this total series of 230 specimens that the variation of the juvenile size classes (below 45 mm. snout-vent length) exceeds the variation of all of the adults. It can be inferred that this

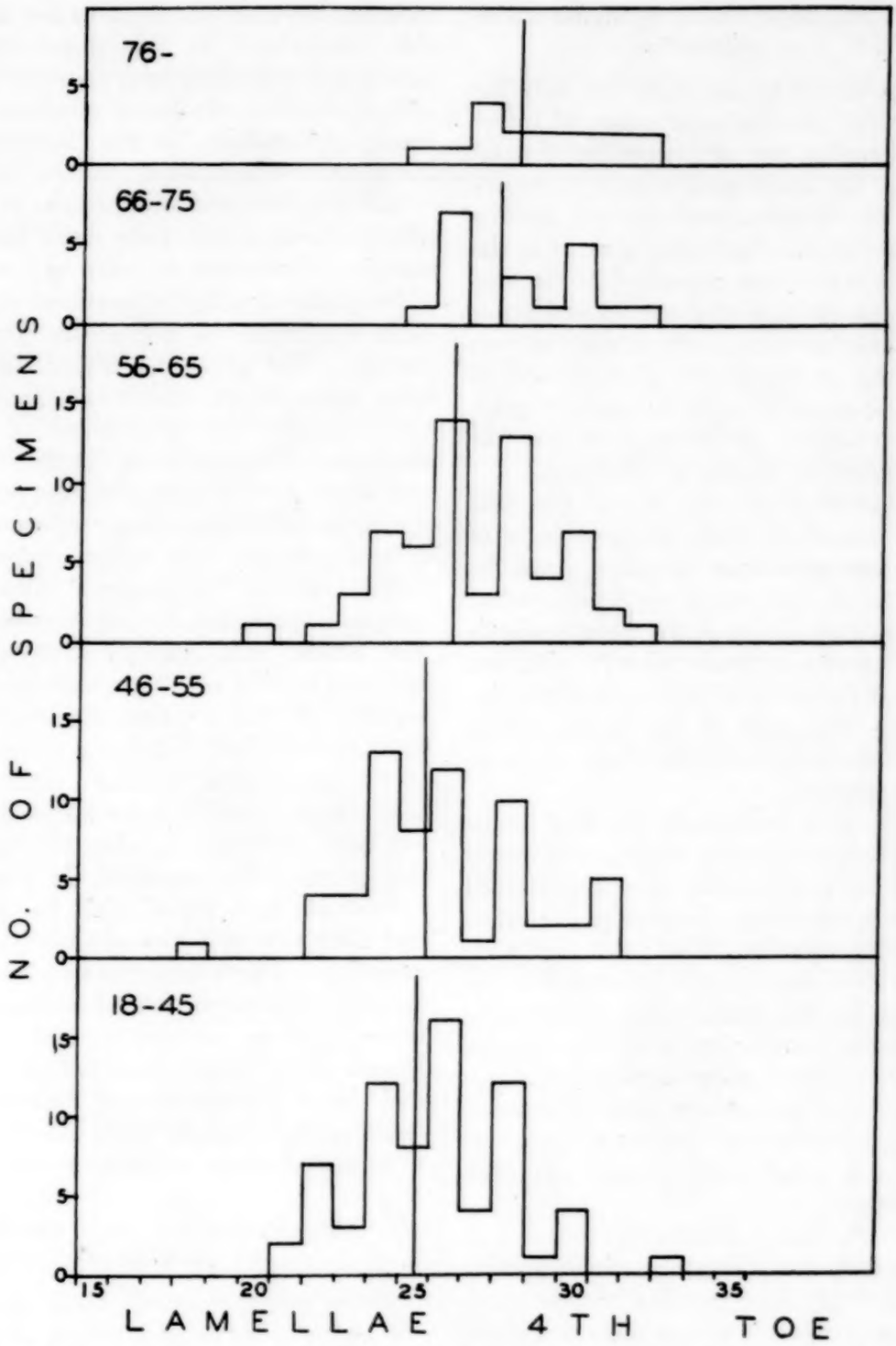

FIG. 6. Differential selection in the number of infradigital lamellae of the fourth toe in the total sample of *A. praesignis*.

phenomenon is not a matter of growth because the variation of the adults is included within and exceeded by that of the juveniles. Furthermore, meristic changes during postembryonic life are not known to occur in reptiles. Observations on young *Aristelliger* have revealed no increase in the number of lamellae after each shedding. As a result it may be concluded that the differences in the variation of the smaller size groups and the larger size groups is the result of differential selection.

The selective significance of higher numbers of lamellae

Hence it may be assumed that only juveniles with the higher number of infradigital lamellae are preadapted to the attainment of maximum size. Juveniles with fewer lamellae are selected against when they attain the critical size. On the basis of the evidence presented by the correlation graph of size of species and number of lamellae (figs. 2–4), it may be concluded that as the weight of the individual increases, there is need for greater gripping surface in order to maintain the same degree of agility in climbing.

Further analysis (fig. 6) of the data reveals that the selective force in favor of the greater number of lamellae is not the same for all size categories. The mean lamellar count of each of the three smallest-size categories increases slowly with size but the differences are not statistically significant. This may be due to the size of the samples comprising the three smallest-size categories.

By the time individuals reach a snout-vent length of 65 mm. selection evidently has become more severe, since at this point there is a significant increase in the mean number of lamellae. There is a high level of statistical significance between the differences in the frequencies of the two largest-size categories and the smaller categories (chi-square value $P < .001$). In these two largest-size categories about one-third of the total variation of the juvenile and small adult classes has been eliminated.

Until the summer of 1950 a series of *Aristelliger* from a single restricted locality large enough to determine whether this selection phenomenon took place at a given locality and in a single more or less isolated population was not available in any museum collection. In that year we collected 53 specimens of *A. praesignis* at Calabash Bay, St. Elizabeth Parish, Jamaica. The data were arranged in the same manner as for the entire species (fig. 7). Here too it can be observed that the variation of the juveniles and small adults includes the total variation of the largest-size categories. In this population the two largest-size categories do not have any individuals with the lower numbers of infradigital lamellae. In the Calabash Bay sample it will be noticed that the variation of the juveniles and small adults is not so wide as the variation of the entire Jamaican sample. Furthermore there are no individuals with the higher numbers of infradigital lamellae of the entire Jamaican sample. The greatest shift of the mean takes place in the 56–65 mm. snout-vent category, after the attainment of sexual maturity. The differences in the frequencies of the three largest-size categories and the two smallest-size categories are statistically significant (chi-square value $P < 0.02, > 0.01$). The higher P value of this sample is probably due to its small size. The above data indicate that selective forces operating on single individuals and populations of this species are affecting the maximal size and frequency distributions of the infradigital lamellae. Differential selection as shown by the above data has not been observed in other characters of this genus. For example, the number of infralabials and supralabials in juveniles and adults of this species show the same variation. There seems to be a more harmonious adjustment in these characters between genetic variability and selective forces. The correlation between maximal size of the species and the number of lamellae indicates the high functional significance of these structures (figs. 2–4).

Counterselection for lower numbers of lamellae

Since selection allows those genotypes for higher number of lamellae to attain a larger size or greater longevity and therefore a longer reproductive period, one would expect those individuals with lower numbers of lamellae to be permanently eliminated. Despite this there is wide variation in the juveniles. Whereas breeding starts at 45 mm. snout-vent size, selection seems not to be effective until individuals attain a snout-vent length of 55

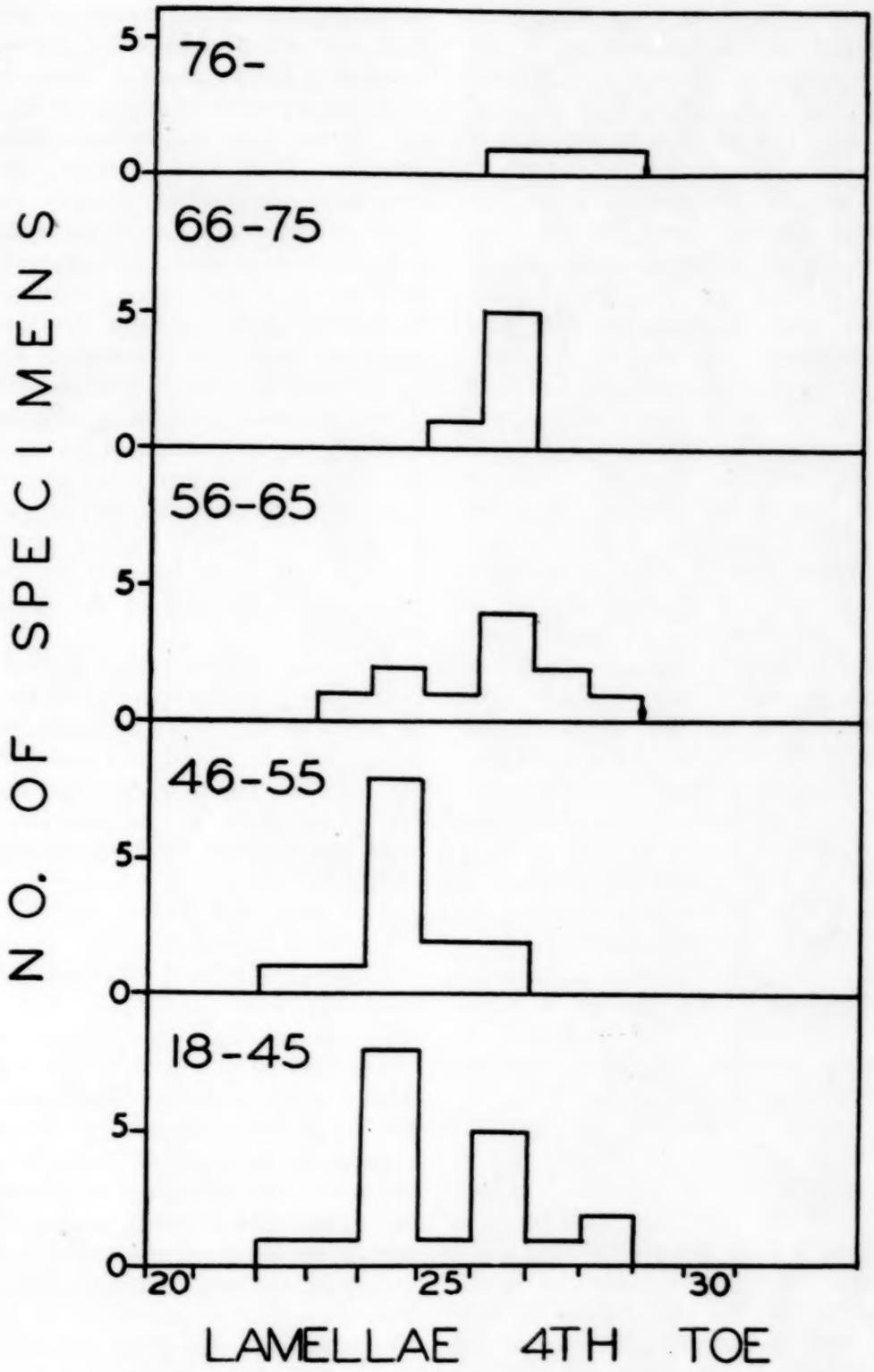

FIG. 7. Differential selection in the number of infradigital lamellae of the fourth toe in a sample of *A. praesignis* from Calabash Bay, Jamaica.

mm. As a result those individuals with fewer lamellae may breed frequently enough to assist in keeping the variability in the juveniles high, despite the fact that the larger individuals presumably breed more often.

In several samples it has been observed that the same type of differential selection

takes place, but in these samples the shift in the mean may not always be in the same size category. In fact the Calabash Bay sample (fig. 7) differs from the total sample (fig. 6) in showing an earlier shift in the means, frequencies and ranges of the lamellae. In other samples from Cayman Brac, Kingston and Morant Cays there are slightly different parameters of juvenile variation, and differential selection takes place in these localities at a larger size class. An analysis of covariance of three samples and the Calabash Bay sample reveals no statistically significant difference in the differential selection in any two localities. This may be due to the small size of the samples. If larger samples become available, it may be possible to show that in different localities differential selection becomes effective at different size classes. If future work shows the differences among populations to be real, then there remains another possible explanation for the observed wide variation of the juveniles; for if small geographic areas have their own characteristic selective pressures (at a given time interval), then migration between areas of intensive selection against low numbers of lamellae to areas of intensive selection for low numbers of lamellae should result in wide variation in the lamellae of juveniles at all localities. This species is widespread in distribution, and domiciliary in habit, and therefore migration between populations may be high, so that if the migration factor is sufficient, then the resulting type of gene flow should insure wide variation of the juveniles. There also remains the possibility that in some areas there is weak selection against small individuals with high numbers of lamellae, thereby limiting the number of individuals that are preadapted to attaining the maximal size of the species. Thus during one period of the life cycle low numbers of infradigital lamellae might be advantageous, whereas in the larger size groups higher numbers of infradigital lamellae are advantageous.

The above hypothesis assumes, and the data seem to indicate, that there is elimination of all individuals capable of attaining large size but who have low numbers of lamellae. Furthermore it assumes that there is a selective advantage in small size and, during early life, to low numbers of lamellae. If it were assumed that two genetically determined growth patterns were present in this species, and that those individuals with more rapid growth would survive only if they had a greater number of lamellae, then the same selection phenomenon would be observed. There is no evidence for this hypothesis, although it does remain a possibility. However, a study of the maturation of the gonads of the species in the genus has shown close correlation (table 1) between reproductive maturity and growth pattern (or regression). This study has not revealed two reproductive patterns in the species, *A. praesignis*.

The data suggest that a conflict of selective forces results in a shift in the means of lamellae frequency through the size categories. It would be expected that if the selective forces all favored the same phenotype then an adjustment would have taken place between genetic variability and the selective forces that would restrict the extent of the juvenile variation.

It seems logical therefore to conclude that there are at least two major selective forces, (1) selection for large size and (2) selection for small size. These selective forces may be in a state of relative equilibrium wherein neither small-size classes nor large-sized classes are favored exclusively in intraspecific competition. Yet the functional advantage of greater number of lamellae prevents large individuals with lower numbers of lamellae from competing successfully with those of equal size that have higher numbers of lamellae. Other available data given below will show the historical aspects of these conflicting forces.

Variation of Body Size

Phylogenetic trends in body size

From the geographic distribution of the genus *Aristelliger* it is evident that *A. praesignis*, the smallest species in the

subgenus *Aristelliger,* is surrounded by related species, all of which attain a greater size. There are at least two explanatory hypotheses. The first and more probable is that *A. praesignis* is descended from a large ancestor and has become smaller. The second is that *A. praesignis* represents the ancestral size and that each of the other species in the subgenus independently became larger. It has been shown that a second species of *Aristelliger, A. titan* Hecht, existed on Jamaica before, and for a short time concurrently with *Aristelliger praesignis.* It may represent the ancestral stock from which *A. praesignis* was derived. The discovery of *A. titan* lends support to the hypothesis that *A. praesignis* was derived from a large ancestor. The *Aristelliger*-bearing fossil layers of Jamaica are actually the remains of owl (*Tyto*) pellet deposits in caves. These may be divided into three groups, the lizard layer, the intermediate layers, and recent deposits. The oldest group, the lizard layer, so called because of the dominant remains, is composed primarily of the anguid genus *Celestus* with a lower frequency of *A. titan.* One of the intermediate layers contains both *A. praesignis* and *A. titan,* but the latter is extremely rare. The recent deposits consist mostly of *Rattus;* the only *Aristelliger* present is *A. praesignis.* The relative frequency of *Aristelliger* in the owl pellet remains has decreased continuously through time with replacement of the larger species by the smaller species (Hecht, 1951). This same phenomenon, of a large sized form being replaced by a smaller form, is also observed in the anguid genus *Celestus.*

A selective factor for small size, the barnowl

An analysis of the recent owl pellet remains from Jamaica shows that the owls feed only on the three largest species of lizards (which are not the most abundant species), and only on the largest-size categories of these lizards (Hecht, 1951). In the recent owl pellets *Aristelliger praesignis* ranks third among the lizards in abundance, and of the individuals represented all remains are of specimens equivalent in size to those exceeding 65 mm. in snout-vent length. These data show that the predator, the barn owl, has selected and is still selecting against large size by feeding not merely on the larger species, but on the largest individuals of that species.

The barn owls have left an historical picture of the effect of this predation. According to Mr. S. B. McDowell, Jr. there are barn owl remains from at least one of the cave deposits in Jamaica (Wallingford Cave, near Balaclava). Not enough is known at this time to determine accurately the size of this owl. It is certain that the size of the owl is an important factor in determining the type of prey and the nature of the cave deposits. It is of interest that Wetmore (1922, 1937) has described two giant fossil West Indian species of barn owls, *Tyto ostologa* of Hispaniola and *Tyto pollens* of Exuma. Wetmore estimates that the Hispaniolan form may have been about 24 inches in length, which is seven inches longer than the maximum recorded for the living species, *Tyto alba* (Bond, 1947). The existence of a large species on Hispaniola suggests that perhaps a similar form of owl may yet be discovered in Jamaica. Unfortunately in the crucial lizard layer collections there are no identifiable remains of a barn owl. The presence of large lizards would indicate a large predator or another technique of feeding, but on the other hand an analysis of the recent owl pellet deposits indicates the same method of feeding on smaller related lizards as is evident in the older lizard layer (Hecht, 1951). From the evidence it is believed that the living species of *Tyto* was probably the predator during the "lizard layer" times, although the possibility remains that a large predator existed. A comparison of the recently extinct mammalian fauna of Jamaica with that of Hispaniola

reveals a marked difference between the two. On Hispaniola there was an abundance of medium sized native histricomorph rodents (*Brotomys, Plagiodontia, Isolobodon*) and insectivores (*Nesophontes*). These mammals lived contemporaneously with, and probably were the prey of, the giant owl (Miller, 1922, 1929). On Jamaica the non-flying land mammal represented in the lizard layer is *Capromys,* another medium-sized histricomorph rodent. All of the *Capromys* represented in the Jamaican fossil owl pellet deposit are young individuals. This indicates that the "lizard layer" barn owl was too small to prey on the adult *Capromys* and therefore must have been smaller than the Hispaniolan *Tyto ostologa.* The lack of an adequate rodent fauna on Jamaica suggests the reason for the unique presence of the lizard layer. In no comparable deposits in Hispaniola, Cuba or Porto Rico is there such a preponderance of lizard remains as in Jamaica. The more recent reduction of lizards as an important part of the prey of the owl may have resulted from the pre-Columbian invasion of *Oryzomys,* the rice rat, into Jamaica and the later introduction of *Rattus* by man.

It is apparent from the studies (Hecht, 1951) made on *A. titan* that almost the entire population of this species was large enough to be prey of the owl. As a result the reduction in size through time of the Jamaican members of this genus has resulted in the escape of most of the breeding population of *A. praesignis* from predation by the owl. It is possible that the invasion of the recently extinct *Oryzomys* and the later introduction of *Rattus* has reduced the selective pressure on the larger *Aristelliger* by offering a more abundant food supply to the owl. Yet before the arrival of these two rodents the large fossil gecko and some of the large fossil anguids may already have been reduced in numbers or become extinct.

The earliest evidence for owl predation on *Aristelliger* is represented by the lizard layer. It is possible to say with a degree of certainty that the lizard layer is not older than the last interglacial and can not be younger than post-Columbian times. It is the author's personal opinion based on the faunal studies of the cave deposits (Koopman and Williams, 1951; Hecht, 1951) that the lizard layer is about ten to twenty thousand years old. If this estimate is correct, then selection for smaller size has been continuous for at least the past several thousand years. It is evident that the evolution of the genus in Jamaica has resulted in reduction of the size of the species with a corresponding reduction in predation by the owls. Despite the continuing selective pressure (by owls and possibly other factors), in apparently one direction, there are still large *A. praesignis.*

Counterselection for large size

From the available knowledge of the life history of *Aristelliger* there are four possible selective factors that may favor large size. These animals have been observed to be territorial in habit. As observed in other lizards (Noble and Bradley, 1933; Evans, 1936; Greenberg and Noble, 1944; Evans, 1951) size undoubtedly is an important factor in the determination of dominance of favorable territory. These crepuscular lizards are known to be vocal. Voice is probably indicative of intense sexual competition, particularly in males. The scarred skins of many preserved large male adults suggest the possibility of sexual combat. Finally larger individuals will have a wider range of food supply, thereby releasing them from competition with the smaller individuals of the same species and the other smaller gekkonid genera of Jamaica. The above evidence for selective advantage of large size is circumstantial but certainly important. In conclusion, it may be stated that there are conflicting selective forces affecting the size and number of lamellae in *Aristelliger praesignis.*

Taxonomic Categories and Selection Phenomenon

This study emphasizes the importance of proper analysis of taxonomic characters and of adequate sampling of different size categories. Poor representation of size classes in samples from different areas of a single species may result in highly statistically significant differences and apparent different frequencies. These differences may be mistakenly assumed to represent subspecific and specific levels of differentiation, when actually they represent selection at different size classes in different localities. In such cases only analysis of juvenile variation will indicate the true status of such populations.

Summary

In lizards of the genus *Aristelliger* there are differential selective forces affecting characters that are functionally important. There is a positive correlation between the number of infradigital lamellae or plates and the minimal breeding and maximal sizes of each species. On the ventral surface of the lamellae beneath the toe there are hair-like structures that are important in relation to the climbing abilities of these geckos. An analysis of the number of plates under the fourth toe in *Aristelliger praesignis* has shown differential selection is affecting the character. The variation of the juveniles and young adults is much greater than that of the largest adult classes. Selection allows only those individuals who can maintain their climbing agility because of their greater number of lamellae to attain large size.

It is suggested that the differential selection shown in the numbers of infradigital lamellae is the result of many selective pressures expressing themselves as selection for or against large size. Only circumstantial evidence such as competition for territory, sexual competition and competition for food is available to illustrate selection for large size.

On the other hand selection against large size is best illustrated by the present and past predation by barn owls. There is good fossil evidence that there has been a continuous selection during the past several thousand years for small size. This is suggested by the extinction of the large *Aristelliger titan,* which may represent the parental stock of the living species. It has been shown that the owl preys selectively upon large lizards, and that in recent owl pellet deposits only the largest *A. praesignis* are represented. This does not mean that predation is the only selective factor against large size, but certainly it is an important one. It is apparent that the living dwarf species, *A. praesignis,* has survived this predation as a result of its evolution towards smaller minimal breeding and maximal size. As a result, predation by owls affects only a small proportion of the total population. This selection for smaller size probably results in selection for lower numbers of lamellae.

There are four conclusions that can be drawn from this study; they are: (1) the adaptive value of a morphological and taxonomically useful character has been demonstrated; (2) conflicting selective forces have been shown to affect the variation of this character; (3) differential selection is not equally effective on all size or age categories of a species; (4) improper analysis of differential selection effects may lead to improper taxonomic conclusions.

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NOTES AND COMMENTS

THE BRIJ HYPOTHESIS AS AN EXPLANATION FOR THE TROPICAL FAUNAL SIMILARITIES BETWEEN THE WESTERN GHATS AND THE EASTERN HIMALAYAS, ASSAM, BURMA, AND MALAYA

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The existence of the tropical faunal similarities between the Western Ghats on one hand and the eastern Himalayas, Assam, Burma, and Malaya on the other has been known for some time (Medlicott and Blanford, 1879). Obviously the animals which both areas have in common must have once had a more or less continuous distribution even though the present intervening drier area is about 1,500 miles in width. In general, the Western Ghats populations display very little differentiation from their eastern counterparts (Blanford, 1901; Ferguson, 1903; Ali, 1935; Ali, 1949; Ripley, 1949; and Hora, 1949b). This fact leads us to believe that the complete break between the two areas must have occurred at a relatively recent date. However, much work on the distribution and taxonomy of the fauna of both areas needs yet to be done for an accurate understanding of the exact relationships between these two areas.

Hora (1949) mentions several hypotheses that have been proposed in the past to account for these faunal similarities. He disposes of all but one of these hypotheses for very evident and understandable reasons. The one remaining hypothesis, for which he cites no author, is entitled the Continuous Range Hypothesis. Apparently there is little disagreement with this, but one should remember that the "continuous" range probably always contained small gaps and while it was disappearing it almost certainly contained gaps of varying magnitude which acted as sort of a selective filter on the fauna. The main speculation involved regarding the explanation of these faunal similarities is the location of the former ecological connection.

Hora proposed the Satpura Hypothesis, as a result of his work on the torrential fishes of the area in question, in which he attempts to explain the existing similarities between the two widely separated faunas by presupposing certain past modifications of the present Vindhya-Satpura trend of hills which loosely connect the eastern Himalayas with the west coast of India (fig. 1). He believes that this range of hills was the connecting link that existed in the past between the east and the west. The Satpura Hypothesis depends upon the following four conceptions (Hora, 1949):

"1. Continuity of the Vindhya-Satpura ranges with the Assam Himalayas in the east and the Western Ghats in the west.
2. Five to six thousand feet elevation of the Vindhya-Satpura ranges and of the northern section of the Western Ghats.
3. Continuity of an ecological belt of mountains with rainfall of about 100 inches or above and consequently of tropical evergreen forests between the Assam Himalayas and the mountains of Ceylon *via* the Vindhya-Satpura Trend and the Western Ghats.
4. Dispersal of the fauna from east to west and the consequent changes in topography necessary therefor."

The first three of these conceptions are by no means conclusively supported by geological evidence (Auden, 1949). The present height of this Satpura Trend is not over about 4,000 feet and is broken in many places. It would have taken a phenomenal amount of erosion during a relatively short period of time to account for the presence and subsequent break in any continuous ecological belt caused by this trend. This seems like poor evidence upon which to build a theory of former ecological connection between the Himalayas and the Western Ghats.

Randhawa (1945) brings to our attention the fact that India, just to the north of the Satpura Trend was, in *historical* times, very much wetter than it is at the present time and supported a typical wet tropical fauna and flora. This fact has apparently been known to archaeologists for some time but zoologists have not paid sufficient attention to it.

Randhawa bases his conclusions on a variety of evidence. Several excavations in the Brij districts of central India, including many about Mathura, have unearthed examples of ancient sculpture that clearly shows several species of trees characteristic of the wet tropics. Four of the most often depicted trees are the Asoka, *Saraca indica;* the Kadamba, *Anthocephalus indicus;* the Champak, *Michelia champaca* and the Nagkesar, *Mesua ferrea* (fig. 1). These trees are found at present in the wet tropics of the eastern Himalayas, Assam and Burma as well

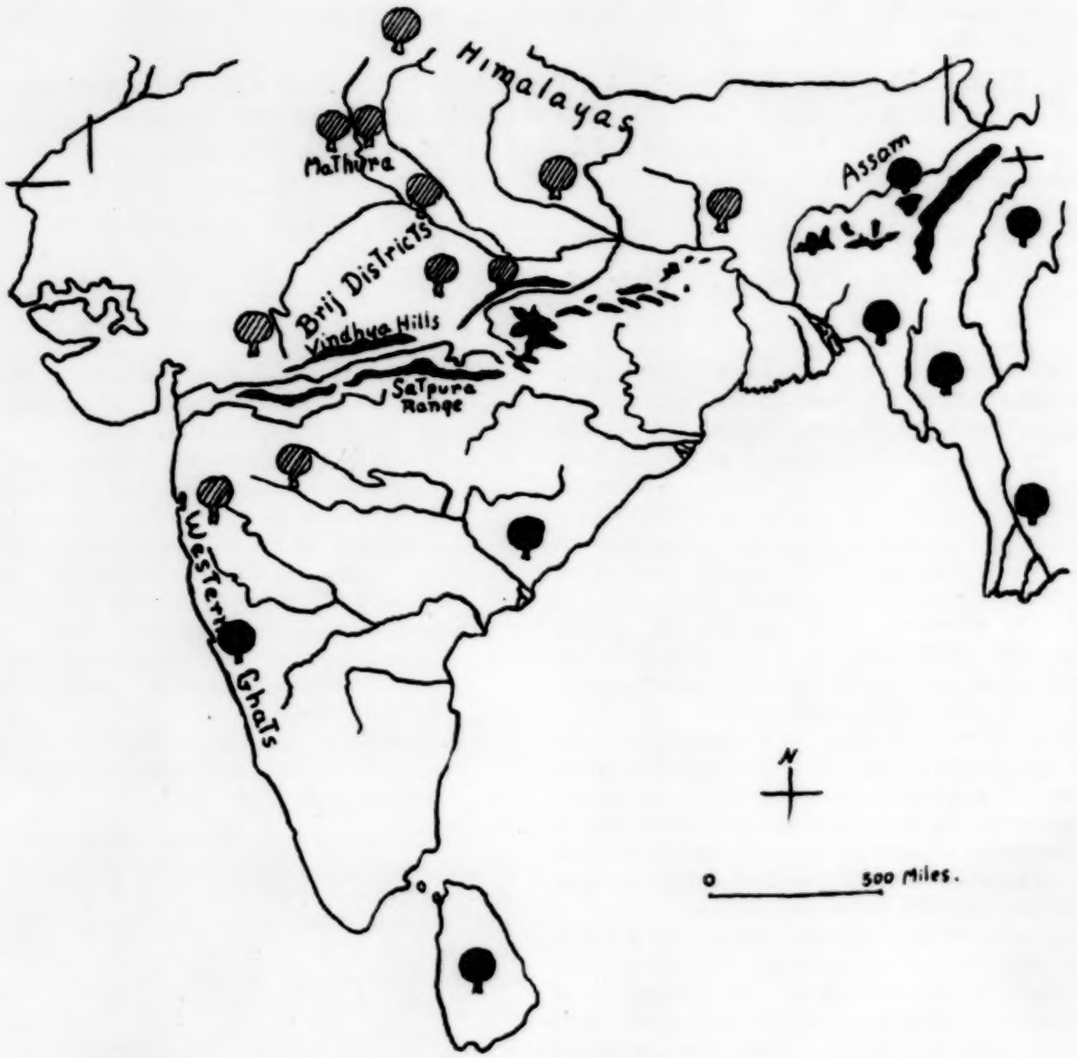

FIG. 1. Map showing the Vindhya-Satpura Trend of hills and the past and present distribution of the Asoka, *Saraca indica;* the least tolerant to dryness of all four trees mentioned in the text (Randhawa, 1945). Past distribution of *Saraca indica* (Randhawa, 1945) indicated by the shaded and solid symbols. Present distribution indicated by the solid symbols, only.

as in the Western Ghats; thus they have a distribution similar to that of the animal anomalies we are interested in. The Kadamba, the most tolerant to dryness of the four species, is found today in isolated, rapidly disappearing, relict populations here and there in the Mathura district. Sanskrit literature tells of festivals in the Brij area where the people collected Asoka flowers and decked themselves with them. Randhawa goes on to cite other evidence of wet tropical flora and fauna having existed throughout the Brij districts in recent times. At the end of Randhawa's paper is a paragraph which vividly portrays these stupendous changes that have recently taken place in the Brij area:

"The 'Brij' country which was covered with luxuriant evergreen tropical forests of *Saraca indica, Mesua ferrea* and *Anthocephalus indicus* about 2000 years ago has completely changed now. The jungles which were the abode of the rhinoceros and the wild elephant, have disappeared, and in their place we find sandy wastes haunted by flocks of black buck and chinkara deluded by mirages of rivers and lakes which exist no more. The ponds and lakes which were visited by ducks and wild geese providing inspiration to the Kushana sculpture, have completely disappeared, and in their place we see ravines, sand dunes and parched plains which have become the rendezvous of the Grey Partridge (*Francolinus pondicerianus* Gmelin.), quail (*Coturnix coturnix* Linn.) and the sand grouse (*Pterocles exustus* Temm. and Lang.) the typical birds of the Rajputana desert."

The writer believes, then, that in view of the above evidence showing the existence of a former wet tropical belt across India between the eastern Himalayas and the west coast north of the Vindhya-Satpura Trend that this was the area that once supplied the connecting link between the now anomalous faunas. Since this connection existed during historical times the small amount of differentiation now found between many of the eastern and western forms is perfectly understandable. Some of the present subspecific, or even specific, differences might be explained by the interruption of possible clines existing through the former area of occurrence, although undoubtably repeated separation and incomplete colonization of the intervening area had a great deal to do with shaping the faunal picture as we see it today.

The distribution of torrential stream fishes, upon which Hora has based his hypothesis, requires a more or less continuous connection of torrential streams that may or may not depend upon wet tropical conditions. A connecting ecological area that would facilitate the movements of terrestrial animals need not involve drainage systems at all. The writer's Brij Hypothesis does not depend upon drainages to explain the terrestrial faunal similarities of the two areas under discussion here. This still leaves the torrential fish anomalies to be explained. The answer to this may lie in an investigation of stream capturing and subsequent changes of direction of the fresh waters of peninsular India.

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THE IMPORTANCE OF THE NERVOUS SYSTEM IN THE EVOLUTION OF ANIMAL FLIGHT

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Introduction

In order to be able to fly, an animal must not only be able to support its weight but must also be able to control its movements in the air. Since animals do not have to learn to fly, or at most need only to perfect by practice an ability already present, it follows that there has been evolution of the sensory and nervous systems to ensure the correct responses in flight. Although no direct evidence on this point can be obtained from fossils, something can be deduced from the gross morphology of primitive flying animals. This can best be done by comparison with the control of aeroplanes, since the latter problem is well understood.

The stability of primitive flying animals

If an aeroplane is to be controlled by a pilot, it must be stable. An aeroplane, or a gliding animal, is stable if, when it is disturbed from its course, the forces acting on it tend to restore it to that course without active intervention on the part of the pilot in the case of an aeroplane, or without active muscular contractions in the case of an animal. Although gliding has probably always preceded flapping in the evolution of flight, stability can also be defined for flapping flight. In this case, there is a continuous series of muscular contractions. We may say that such an animal is stable if the forces acting on it tend to restore it to its course without any modification of that cycle

of contractions being required. In practice the most important type of stability is that for rotation about the pitching axis; i.e., a horizontal axis normal to the flight path. In both gliding and flapping flight, stability in pitch can be ensured by the presence of an adequate horizontal surface behind the center of gravity.

The stability defined above is referred to as static stability. The response of a stable aeroplane to a disturbance may be a deadbeat subsidence or an oscillation. Such oscillations will normally be damped, but in rather special circumstances long period oscillations may be divergent. Such divergent oscillations can normally be controlled by a pilot, and it seems unlikely that they are of any great importance in animal flight. The response of an unstable aeroplane to a disturbance is a divergence, whose rapidity depends on the degree of instability.

Flight has been perfected by four animal groups, the birds, bats, pterosaurs, and insects. Too little is known of the postcranial skeleton of primitive bats for them to be discussed with any certainty. However, it is generally assumed that the bats have been evolved from gliding arboreal mammals functionally similar to the modern cobego *Cynocephalus* (syn. *Galeopithecus*), although there is probably no phylogenetic relationship. In this mammal the patagium forms a web connecting the fore and hind limbs, and extending backward as the interfemoral membrane to include the tip of the long tail. There can be little doubt that it is a stable glider. In the bats the length of the tail, and therefore the size of the interfemoral membrane, is reduced, and the forelimbs are greatly elongated. These changes have the effect of shifting forward the horizontal lifting surfaces relative to the center of gravity and thus reducing stability.

In the other three groups, there are good reasons to suppose that the earliest forms were stable in the sense defined above. The Archaeornithes possessed a long tail bordered on either side by a row of feathers, the whole forming a very effective stabilizing surface. In the case of the pterosaurs, the earliest known forms from the lower Jurassic belong to the suborder Rhamphorhynchoidea. These forms had a long stiff tail which in at least one genus, *Rhamphorhynchus,* is known to have terminated in a stiffened fluke of skin. This tail must have had a stabilizing function. However, the latest worker on these fossils, Gross (1937), believes that the fluke of skin was disposed in a vertical plane. If this is the case, it would have acted as a stabilizer for yawing rotations, i.e., rotations about a vertical axis. It would, in fact, be analogous to the fin of an aeroplane rather than to the tailplane. This, if confirmed, is a rather surprising fact, since in an aeroplane, although both pitching and yawing stability are necessary, instability in pitch renders an aeroplane more completely uncontrollable than instability in yaw.

There are also several features of fossil insects from the Carboniferous to suggest that they were stable. The oldest and most primitive order of winged insects is the Palaeodictyoptera from the lower and middle strata of the upper Carboniferous. They possessed an elongated abdomen, each segment bearing conspicuous lateral lobes, thus forming an effective stabilizing surface. There was also a pair of slender and often greatly elongated cerci. Although such structures would be ineffective as stabilizers on an aeroplane, they are probably quite effective on an insect, due to the greater importance of air viscosity on a small scale (scale in this sense being measured as the product of length and forward speed).

The evolution of instability

It appears, therefore, that primitive flying animals tended to be stable, presumably because in the absence of a highly evolved sensory and nervous system they would have been unable to fly if they were not, just as a pilot cannot control an unstable aeroplane. It is, however, theoretically possible to design an automatic pilot to fly a fundamentally unstable aeroplane. In spite of the obvious practical objections to such a scheme, it would have certain advantages. The first is that an unstable aeroplane could be turned more rapidly. The second advantage lies in the fact that in a stable aeroplane the stabilizing tailplane plays a relatively small part in supporting the weight. In an unstable aeroplane, on the other hand, the elevators would be lowered as the plane flew slower, the tailplane would, therefore, support a larger part of the weight, and thus a lower flying speed could be attained without stalling. (The stalling speed is the minimum speed at which an aeroplane can fly.)

Now it is clear that the practical objections to such a scheme as applied to aeroplanes do not arise in the case of animals. There is, in fact, good evidence that birds do not need to be stable in order to fly. In some birds there is no tail in an aerodynamic sense at all. Other birds, which normally possess a tail, can fly without it; this can often be observed in the case of sparrows which have completely lost their tails. In fact, in most birds the tail does not seem to act as a stabilizer, but as an accessory lifting surface when flying slowly. This can be observed, for example, in the case of gulls. These birds open their tails only when turning sharply or flying slowly. It can then be seen that the slower the bird flies the more

the tail is lowered; as mentioned above, this is characteristic of the unstable state.

No such detailed discussion is possible in the case of the pterosaurs, but it is significant that the later upper Jurassic and Cretaceous Pterodactyloidea completely lacked a tail.

In the case of insects, it is impossible to make any generalizations, since there is such a wide adaptive radiation within the group. It is probable that some orders, e.g., the Ephemeroptera, are stable. However, in the case of the Diptera the work of Hollick (1940) and Pringle (1948) has shown the importance of the arista and halteres during flight. Indeed, in the case of the Diptera, so far from being stable, the forces acting on a fly are not even in equilibrium in the absence of sensory input from the arista, and muscular response to this input.

To a flying animal there are great advantages to be gained by instability. The greater manoeuvrability is of equal importance to an animal which catches its food in the air and to the animals upon which it preys. A low stalling speed is important in a number of ways, and particularly to larger animals. For a set of geometrically similar animals, the stalling speed increases as the square root of the linear dimensions. Therefore a successful landing may be possible in the case of a large animal only if it can reduce its stalling speed, and instability is one of the ways in which this may be done. The account given above of the way in which gulls use their tails illustrates this point. Thus it is possible that the evolution of a pterosaur as large as *Pteranodon* depended on the prior evolution of instability. In extreme cases a lower stalling speed may make hovering flight possible.

It is also important to realize that we are not concerned with a change from stability to instability which must be made in a single step. Any reduction in the degree of stability will be an advantage provided there is a parallel increase in the efficiency of control. This can be seen by analogy with aeroplanes. Transport aeroplanes are normally designed with a fairly high degree of stability, since safety in steady flight is of greater importance than manoeuvrability. In fighter aircraft, however, manoeuvrability is of first importance, and the stability margin is usually reduced to a minimum. It is therefore, possible to see how instability may have been evolved gradually.

Palaeontologists will have to solve the question of the relative times taken to evolve stable flight, with the relatively coarse controls needed for it, from walking and climbing; and of unstable from stable flight. Unfortunately we only know Archaeornithes from one horizon; on the other hand the Rhamphorhynchoidea persisted for a time measured in tens of millions of years, as did the stable Palaeodictyoptera. It is possible that the evolutionary changes needed for stable flight could be made rather quickly, while the nervous and sensory adjustments needed for unstable flight were inevitably slower. If, as is also possible, the bats evolved rather quickly to instability, this may be due to the greater adaptability of the mammalian brain.

If the conclusions of this paper are accepted the study of the remains of primitive flying animals, and even experimental studies on full-scale models of them, will acquire a special importance as throwing new light on the functional evolution of nervous systems.

There are, of course, several other cases where similar deductions can be made as to the evolution of systems of which no direct fossil evidence exists. Among the most obvious is the need for a highly developed vasomotor system in large land animals which change their posture. A dinosaur standing on its hind legs without the previous evolution of such a system would have suffered from cerebral anaemia. However, it is doubtful whether the palaeontological evidence for such evolution is as clear in any other case as in that of flight.

Summary and conclusions

Stability in gliding and flapping flight is defined. It is argued that the earliest birds, pterosaurs, and flying insects were stable in the sense defined. This is believed to be because in the absence of a highly evolved sensory and nervous system they would have been unable to fly if they were not.

The advantages of instability to a flying animal are discussed. It appears that in the birds and at least some insects, and probably in the later pterosaurs, the evolution of the sensory and nervous systems rendered the stability found in earlier forms no longer necessary.

Acknowledgments

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SPECIES STATUS OF THE BLOCK ISLAND FIELD MOUSE, MICROTUS PROVECTUS

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Islands have been colorfully described by Dr. Ernst Mayr as evolutionary traps which if large enough may permit the survival of certain aberrant forms but if small may be an extremely important factor in the process of extinction. Some populations inhabiting small islands, however, manage to survive in spite of the fact that they may be living a genetically precarious existence. Rarely, however, are distinct species found among these insular fauna.

Several kinds of mice which inhabit the small islands of Pleistocene origin adjacent to the southern shore line of New England have been described as true insular species on the basis of morphological differences which exist between them and their mainland relatives. It is the purpose of this preliminary report to communicate some of the results obtained in attempting to test the validity of the species status given to the Block Island field mouse, *Microtus provectus*. The basis for naming this insular mouse a separate species has rested simply upon certain small morphological features in the skull and upon a body size described as somewhat larger than its mainland relative, *Microtus pennsylvanicus* (Bangs, '08). It is evident that these are rather meager data on which to establish a separate species. Although morphological variations are sometimes reliable in determining species, physiological differences, if they can be found, are of infinitely greater value. It was, therefore, of considerable interest to learn the extent to which geographical isolation might have resulted in sexual isolation between *M. provectus* and *M. pennsylvanicus*.

From animals trapped originally on Block Island and in the vicinity of New London, breeding colonies of both species were established before any attempts at hybridization were undertaken. To date it has been possible to make six different matings: five between *M. pennsylvanicus* females × *M. provectus* males and one reciprocal cross between a *M. provectus* female × *M. pennsylvanicus* male. Among the crosses between mainland females and insular males, one has resulted in the production of a litter of five hybrid offspring. Another female, although kept with an insular male for a period of twenty-one days, produced no offspring; the same female, mated to a second insular male was killed by him two weeks after they were placed in the same cage. A similar fate was met by a third mainland female mated to a different Block Island male. Attempts at copulation were observed between a fourth mainland female and insular male (male, parent of litter mentioned above) but unfortunately the female escaped from her cage and died soon after recapture. No results were obtained from the mating between the *M. provectus* female × *M. pennsylvanicus* male although this female has produced several litters when mated to a *M. provectus* male.

At this time it seems best to reserve a discussion concerning the possibility of the evolution of partial sexual isolation between the mainland and insular populations of Microtus; additional data are in order before this can be established. The evidence, however, does have considerable bearing upon the species status of the insular mice.

Dobzhansky points out emphatically that the attainment of the stage of the evolutionary process at which fixation of complete physiological isolation takes place is fundamentally important in signifying the advent of species distinction but one must determine whether mere geographical barriers prevent a natural gene exchange between two populations or whether the lack of hybrids in nature is due to fundamental physiological differences intrinsic within the populations. The production of some hybrids between insular and mainland *Microtus* is a strong indication that natural hybrids are prevented merely by geographical rather than by physiological isolation. It does not seem legitimate to conclude that this is merely an instance of bringing together two species from nature which under laboratory conditions produce hybrids. The results of a more thorough study of the morphology of *M. provectus* and *M. pennsylvanicus*, to be published at a later date, do not appear to provide any additional reasons for considering the Block Island fauna distinct from *M. pennsylvanicus*. It, therefore, seems best at present to regard the insular and mainland forms of *Microtus* as identical species. Whether or not the island form should receive the distinction of being an insular race (subspecies) rests upon the results of investigations now in progress concerned with growth rate differences which may exist between *M. provectus* and *M. pennsylvanicus*.

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COMMENTS ON LITERATURE IN PLANT EVOLUTION

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Evolution and breeding of cultivated plants. The great contributions of N. I. Vavilov to plant breeding are well known to geneticists, and are vividly described in the biographical sketch by Dobzhansky in the Journal of Heredity for 1947, vol. 38, pp. 227–232. From his wide experience with the diversity of cultivated plants in all parts of the world, Vavilov made several important generalizations about their evolution, the best known of which are his "Law of Homologous Series in Variation," and his ideas about the relation between centers of variability and centers of origin. Up to the present, this work has been available to readers not acquainted with the Russian language only in three widely scattered publications; an article in the Journal of Genetics for 1922; a book, "The Origin of Cultivated Plants" (1926), containing a complete English translation of the Russian text; and a short article in "The New Systematics," edited by Julian Huxley (1940). Now, however, we have in a single volume a first class translation of Vavilov's final publication of these ideas, which appeared in Russian in 1935.[1]

Of the four articles included in this volume only the first two are of interest to the evolutionist. In "The Phytogeographic Basis of Plant Breeding," Vavilov presents again the theory which was first elaborated in "The Origin of Cultivated Plants," namely, that for all species of cultivated plants there exist centers of genetic diversity, and that usually these centers are the regions in which that crop originated. In the article under review, eight such centers are recognized, and for each of them a large number of species is listed. For instance, 136 species are listed as having originated in the Chinese center, 117 species in the Indian center, and 83 species in the Near-Eastern center.

The first feature which strikes the reader about these centers is the large area which each center occupies. As shown on the map which accompanies the article, the larger centers are thousands of square miles in extent. In fact, the boundaries of the five Eurasian centers are nearly contiguous with each other, and their combined area includes almost all of the arable land in Eurasia situated south of the 40th parallel of latitude. For this reason, the delimitation of these areas does not designate very exactly the place where each of the crops was first cultivated, and it is possible that different species listed from the same "center" were actually first cultivated in localities several hundred miles apart from each other. This broad delimitation is as it should be, considering the difficulties involved determining the place of origin of any plant species, wild or cultivated.

A second, more serious problem concerns the differentiation between primary and secondary centers of varietal origin. Vavilov recognizes that some centers of diversity may be "secondary centers of varietal origin," and lists Spain as an example in the case of wheat. He suggests (p. 18) that these secondary centers may be recognized because "the number of subspecies within the separate species . . . is very small compared to the number found in the real centers of initial formation of these species." The difficulty with this criterion is that it depends upon one's definition of species and subspecies, which is a particularly troublesome problem in cultivated plants. Furthermore, some of the centers considered by Vavilov as primary are far from the regions considered by other authors to be the centers of origin for the same crop. Thus, Vavilov regards Ethiopia as the center of origin of cultivated barley, while the more recent work of Åberg (Symb. Bot. Upsalienses, **4** (2): 1–156, 1940) points to central Asia as the center of origin for this crop. The center for maize is regarded as Mexico and Central America, in contrast to the opinion of Mangelsdorf, that maize originated in South America. In fact, there is nothing in Vavilov's evidence which would make impossible or even improbable the opinion of Schiemann (Naturwissenschaft, **27**: 377–383; 394–401, 1939), that centers of genetic diversity in cultivated plants occur as frequently or more frequently at the periphery of their range, as in their centers of origin, and are largely the result of isolation combined with

[1] Vavilov, N. I. The origin, variation, and breeding of cultivated plants. Translated by K. S. Chester, 1950. Chronica Botanica, Vol. 13, no. 1/6 (pp. vii–366). Waltham, Mass., Chronica Botanica Co.; New York City, Stechert-Hafner, Inc. $7.50.

relaxation of artificial selection due to primitive methods of agriculture. The centers of diversity recognized by Vavilov are of great importance to the plant breeder, since they are the best sources of breeding stock; but Vavilov's discussion of their evolutionary significance seems to this reviewer less and less convincing as the years go by.

The second article in the volume under discussion is an expansion of Vavilov's publication of 1922 on the law of homologous series in variability. More factual data are included, and the theoretical account is expanded to include a definition of species and of intraspecific variability in terms of this "law." The "law" is, however, no more than a descriptive generalization to cover certain phenomena which previously had not been brought sufficiently clearly to the attention of botanists. It states simply that intraspecific variations run parallel to each other in related species. Vavilov does not speculate on the possible causes for this parallelism, but at least three causes can be suggested. First, if two species resemble each other in their general architecture, their variants which have desirable qualities are likely to be similar. Second, related species, where studied genetically as in *Drosophila*, have homologous gene loci, which are likely to mutate in the same direction. Finally, the developmental pattern of related species is similar, so that the types of mutations which produce harmonious alterations of these patterns are likely to be similar also. Any or all of these factors could be responsible for the homologous series observed by Vavilov.

Vavilov's monumental work has long been of prime importance to plant breeders, and the present volume will be of greatest value to them. His evolutionary generalizations have been of value chiefly in calling the attention of botanists to certain phenomena which need explanation.

The evolution of plant species. The most comprehensive and thorough experimental research on the evolution of the higher plants which has yet been carried out is undoubtedly that of Dr. Jens Clausen and his collaborators at the laboratory of the Carnegie Institution of Washington, Stanford, California. Their work on the differentiation of ecotypes within such species as *Potentilla glandulosa* and *Achillea borealis* has already been published in detail and has received world wide acclaim. On the other hand, their equally extensive research on species differentiation in the California tarweeds (tribe Madiinae, family Compositae) remains largely unpublished. All students of plant evolution will therefore welcome a new compact volume which graphically summarizes the most important data obtained from both of these lines of research, and integrates them with earlier studies made by Dr. Clausen on the genus *Viola*.[2] In addition, this volume discusses the theoretical implications of the results obtained. For these reasons, it must be ranked as one of the most important contributions to our understanding of plant evolution which has appeared in recent years.

The new data on the Madiinae include descriptions of intraspecific racial differences which supplement those on *Potentilla* and *Achillea* in that they deal with annual species which, though widespread geographically, are confined to a single climatic zone, and they place greater emphasis on differences in the reproductive characteristics of flower and fruit than was done in the above mentioned perennial genera. In all of these groups, however, the primary objects of study have been character complexes in local populations. Where emphasis was placed on the distribution of single characters over several populations, no evidence of character gradients, or clines, was found, and Dr. Clausen minimizes the importance of such gradients. In this reviewer's opinion, however, this may merely reflect the character of the material which has been studied. The apparent absence of clines in species of Madiinae, with their relatively restricted ranges of climatic tolerance and tendency to exist in more or less localized communities, does not mean that clines would not be expected in other species with wider ranges of tolerance and with more continuous populations.

The most valuable data on races of Madiinae were obtained from studies of segregation in the progeny of interracial hybridization. As many other workers have found in other groups, most of the character differences between races are governed by multiple factor inheritance, but there are some striking examples of mono- or bifactorial inheritance. These include the floccosity of the pappus in *Layia platyglossa*, the presence or absence of a pappus in *L. chrysanthemoides*, and the presence or absence of ray flowers and involucral paleae in *L. glandulosa*. These characters are important because they have been extensively used by taxonomists for delimiting species or even genera of Madiinae. In the genus *Layia*, many of the characters considered fundamental by taxonomists may vary within the same population, may be inherited according to a relatively simple genetic mechanism, and from the genetic as well as the evolutionary point of view appear to be far less important and fundamental than are other characters which are often overlooked by taxonomists, but which play an important

[2] Clausen, Jens. Stages in the evolution of plant species. viii–206 pp., 76 figures. Cornell University Press, Ithaca, N. Y. 1951.

role in determining the adaptive value of the races or species in question.

The hybridizations of Madiinae have yielded particularly valuable data on barriers of hybrid inviability, weakness, or sterility which provide the genetic basis for the distinctness of species. Barriers of this type exist between some populations belonging to the same species, although in such instances other populations serve as intermediaries by forming fertile hybrids with both of the two populations which have difficulty in exchanging genes directly. In *Layia glandulosa*, for instance, nine different crossings involving eight geographically separated populations included four which were fully fertile and vigorous in Both F_1 and F_2, and five which indicated the presence of partial genetic barriers. The degree of interfertility was not correlated with the subdivision of *L. glandulosa* into subspecies on a morphological and ecogeographical basis. In the complex of *Hemizonia virgata*, which apparently should be placed in the genus *Holocarpha*, genetic barriers between populations of an entity recognized by all taxonomists as a single species are particularly prevalent. This group, and in fact several species of the tribe Madiinae, would make particularly favorable material for a study of the genetic basis of the reproductive isolation barriers which separate plant species.

The nature of the isolating mechanisms which separate species is beautifully illustrated by a series of diagrams, or "crossing polygons," for the genera *Layia*, *Madia*, and *Hemizonia*. These show clearly the striking differences between the three genera in the development of reproductive isolating mechanisms, and the astonishing degree to which these mechanisms are developed, even between species which on morphological grounds appear to be closely interrelated.

Dr. Clausen's discussion of these remarkable data is admirable for its balance and conservatism, but disappointing in its brevity, and in the indefiniteness of his working hypothesis to explain how the barriers of reproductive isolation arose. This principal argument is as follows (pp. 164–165). A plant species or race becomes adapted to its environment by developing a ". . . delicate physiological system, governed by an equally intricate system of genes," which "must form a workable unit." "Each species has evolved its own kind of genetic-physiologic system, and the systems of some species are so successfully balanced that very marked variations of them can be developed that are able to fit contrasting climates." As an example of the type of balance to which he refers, Dr. Clausen suggests that there may be ". . . series of genes that increase assimilation at a given temperature, balanced against others that may slow the process down." The inviability, weakness and sterility of interspecific hybrids are attributed to the upset of this genetic-physiologic balance, which results from recombining the elements of different systems.

In this reviewer's opinion, this hypothesis raises more questions than it answers. Why should *Potentilla glandulosa* have produced one system which can be modified to suit climatic extremes as great as the Southern California coast and the alpine heights of the Sierra Nevada, while the *Holocarpha* complex, although restricted to a single climatic belt, has evolved scores or hundreds of entirely incompatible physiologic-genetic systems? Dr. Clausen has suggested that repatterning of the chromosomes has been responsible for the barriers of hybrid inviability in *Holocarpha*, but this hypothesis does not agree with his data, since types with apparently very different chromosomes (and somewhat different ecological preferences) form vigorous hybrids, while other types with very similar chromosomes and almost identical ecological preferences cannot be crossed at all. Furthermore, in other genera, such as *Oenothera*, extensive chromosome repatterning has not interfered at all with the ability of forms to intercross. Also, Clausen's hypothesis fails to explain examples such as *Layia glandulosa*, in which populations belonging to morphologically different subspecies and adapted to different habitats may be completely interfertile, whereas other populations which are morphologically indistinguishable and ecologically nearly equivalent form partly sterile hybrids.

Perhaps we are not ready for answers to these questions. In the concluding statement of his book, Dr. Clausen remarks: "Faced with such a situation, the scientist becomes humble, for at this point he meets the Great Unknown." But there is no doubt that the final answers will come largely through the patient labors of scientists like Jens Clausen, who have the insight to recognize the problems to be solved, and the humility to realize that their solutions will not come quickly or easily.

COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY
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ORIGIN AND EVOLUTION OF MAN

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In turning to the Table of Contents of this volume, it is pleasant to be able to note immediately that, as contrasted with previous volumes, the somewhat pernicious custom of publishing papers in alphabetical order of author's name is abandoned. Instead, emphasis is withdrawn from the authors to the topics under discussion, which is as it should be. The subject of the origin and evolution of man is divided into seven main topics as follows:

1. Population as a unit of study;
2. Origin of the human stock;
3. Classification of fossil men;
4. Genetic analysis of racial traits (which in turn is subdivided into three groups of talks);
5. Race concept and human races;
6. Constitution;
7. Perspectives of future research.

Counting the subject of genetic analysis of racial traits as three discussion groups, each of the nine sets of papers was presented on a separate day, and the subject of each was summed up by the chairman for that day, his remarks being published in the appropriate sections. The result is an unusually well ordered and useful presentation of the subject which resolves itself into what might almost be considered an advanced textbook of modern aspects of human evolution.

The first day's discussion, "Population as a Unit of Study," stands as an introduction to the remainder of the symposium. Strandskov, in a discussion of the effect upon human evolution of various types of mating systems involving such factors as random mating and nonrandom mating, inbreeding and outbreeding, the effects of mutation, migration, and isolation, concludes with a brief and pithy summary of the basis of human evolution which is so well put that I think it worth quoting here.

"1. The machinery of heredity of man is similar to that of other sexually reproducing plants and animals.

"2. Man has evolved from some other species of primate.

"3. The raw materials of human evolution have been and are primarily small genic mutations.

"4. Pre-human and human genic mutations were and are fortuitous and not guided in their direction by any mystical or supernatural force.

"5. Natural selection has been and is the primary guiding factor of human evolution.

"6. Man has evolved unique human characteristics not possessed by any species of animal, but these have appeared as a consequence of the same evolutionary processes as have given rise to unique characteristics among other forms of life.

"7. Some of man's unique characteristics are affecting the usual operation of natural selection insofar as it pertains to human evolution and are giving the direction to human evolution which is not the most favorable from a survival point of view.

"8. Man must accept his origin from some other species of primate and also his present biologic status, but he need not accept completely his present evolutionary trend. It is within his power to redirect to some extent the present and future course of his own biologic evolution."

Point 7 is somewhat cryptic, but in the body of the paper Strandskov quotes Muller to the effect that special agents such as X-rays, ultraviolet light, and certain chemicals which are not ordinary components of the environment but rather specialized productions of human society may be acting to increase the mutation rate among human beings in the same manner that experimentally they have been shown to increase the mutation rate among lower organisms. Since random mutations are not ordinarily for the better, this could be a dangerous trend.

Buzzati-Traverso and Thieme in successive papers discuss what might be called the strategy and tactics, respectively, of population surveys with a view to determination of their genetic characteristics. Buzzati-Traverso stresses the difficulties of determining what a "unit of population" might be in a species such as Homo sapiens, which is continuously distributed over the surface of the earth, and among the various groups of which intermixture is constant. After considering various factors which affect human evolution, he concludes that natural selection is the most important factor in the evolution of man as it is for other organisms. Man's ability to control his environment, and thus decrease the effectiveness of natural selec-

tion, is not yet, in Buzzati-Traverso's opinion, sufficient to play a significant role.

Thieme describes in detail the determination of various bodily measurements in the Puerto Rican population with averages given for both males and females in four different nutritional classes. In so doing, he details the difficulties of selection and the large amount of background information necessary before a basic sample structure can be designed. Thieme considers that in large populations a goal of one per cent of the parent population should probably be a minimum number for a survey.

The second group of papers begins with a presentation by Schultz of "Specializations of Man and his Place Among the Catarrhine Primates." The data presented show man to have followed a line of evolution common to all the great apes. In some features of his development, he has progressed further from the ancestral characteristics, but in others he has not, or even perhaps lagged behind. The factors in which man has progressed further than any of the apes are the prolongation of the main periods of life (since both the period of maturation and the length of life as a whole are at least twice as great as among the anthropoid apes), the enlargement of the brain, and the erect position of the trunk with the subsidiary adaptations that accompany these. Furthermore, he is less hairy than the apes. In other respects, such as—to cite one example—the number of lumbar vertebrae, the orang-utang, chimpanzee, and gorilla have all become specialized to a greater extent than has man. Whereas old-world monkeys have seven vertebrae, man has five, the orang-utang four, and the chimpanzee and gorilla less than four.

One unfortunate aspect of Schultz's paper is the figure on page 41, in which the trunk skeletons for certain organisms are adjusted to the same total length and compared. These are listed both in the figure and in the caption as the macaque, gibbon, Negro, and chimpanzee. Why it should be felt necessary to stipulate that the human skeleton is that of a Negro is a mystery to the reviewer. The difference between the skeleton of a Negro and that of a white man is surely negligible, particularly when it is being compared to apes and monkeys.

Simpson, in the next paper, takes issue with certain fallacies in regard to evolution—particularly with orthogenesis or the rather mystical belief that a direction of evolutionary change, having once begun, must continue in the direction of specialization to extremes more and more unwieldy and ridiculous, and finally to racial extinction. He also points out the fallacy of that particular form of orthogenesis which assumes that with time species grow larger, and that of two related fossils—one of which is larger than the other—the larger must be the later. The care which must be taken in the interpretation of evolutionary trends because of the phenomena of convergence, divergence, and parallelism is also discussed.

Washburn, in the paper entitled, "Analysis of Primate Evolution," decides that the critical primate adaptation initially responsible for the origin of man as a distinct group is in the pelvis. Bipedal locomotion and a truly erect posture come first, with all the secondary changes in thigh, leg, and foot that must have followed. Changes in the teeth, brain size, and many other parts of the body took place later at a slower rate and continued into late Pleistocene times. Washburn points out that with each major advance in primate evolution, the brain doubled or even tripled its size, and that the last doubling took place after early man had become a tool-using animal. This may have sharpened selection and made a final adjustment in brain size fairly rapid.

The next discussion, "Classification of Fossil Man," includes papers by McCown, Stewart, and Mayr on taxonomic problems of human evolution and, to the reviewer at least, seems the most specialized of the entire symposia. Of the three, Mayr's paper is perhaps the most stimulating. He points out the natural tendency of man in dealing with himself and his immediate ancestors to see and stress minute differences that in other species would go unnoticed, or at least be put down as intraspecies variations. The result is that genera and species have multiplied among the Hominidae. Mayr advocates lopping off such taxonomic proliferation and classifying fossil and recent hominids as a single genus, *Homo*, with three species (a) *Homo erectus*, which would include the Java man and the Peking man; (b) *Homo transvaalensis*, which would include the South African apeman; and, (c) *Homo sapiens*, which would include modern man, Cro-Magnon, the Neanderthal, and others. The extent of the simplification suggested may be realized from the fact that no less than three genera and five species of the South African apeman have been described, all of which Mayr would lump as a single species. He suggests the use of trinomials to indicate subspecies differences, as between a Neanderthal man and modern man, for instance. One other interesting point made by Mayr is that human evolution differs from that of other animals in that at no time is more than one species existent. Apparently the advantage of a new hominid species over an old one is sufficiently great so that the newer replaces the older, rather than, as sometimes in other animals, an existence side by side.

The first of the three sessions dealing with the "Genetic Analysis of Racial Traits" deals with the study of the inheritance of pathologi-

cal conditions. Thus, Böök deals with the inheritance of schizophrenia, manic depressive psychosis, and mental deficiency in a North Swedish population, Kemp with a variety of diseases in Denmark, and Neel with thalassemia and sickle cell anemia in Italy and among the Negro populations of America and Africa, respectively. The most interesting point made in these papers concerns the continuous production by mutation of certain congenital diseases which would otherwise not persist because of the high mortality rate. In such diseases an equilibrium exists, depending upon the rate of mutation and the death rate. Where both rates are known, it is possible to estimate the frequency of occurrence of the mutations that cause it. Thus, chondrodystrophy appears once in every 10,000 births in Denmark. Of those affected by it, only one-fifth survive the first year, and the effective fertility of the survivors is considerably reduced. It is calculated that the mutation rate of the dominant gene causing this disease is between eight and a half and ten per 100,000 or between one in 12,000 and one in 10,000 per individual per generation, and between one in 20,000 to one in 24,000 per chromosome generation. The mutation rate for hemophilia per generation is estimated at about one in 50,000, while that for aniridia is about one in 100,000. Kemp states that the rates calculated for the mutant appearance of various congenital and inherited diseases studied fell between one in 10,000 and one in 100,000. Kemp concludes that hereditary diseases are, in many cases although not all, monomeric—that is, dependent upon the change in a single gene. Several hundred such "major mutant genes" have been identified. The hereditary disases caused by the presence of a major mutant gene are usually rare because of the high mortality rate and can only become widespread if the gene is recessive. Inherited predispositions to diseases, on the other hand, are considered by Kemp to be polymeric—that is, dependent upon changes in many genes, so that changes in one or two have little immediate effect, but render mutation the rest of the way somewhat easier.

Neel's paper on thalassemia and sickle cell anemia is parallel to that of Kemp's. In both cases the diseases are considered to be maintained at a more or less constant incidence through the continual incidence of mutations in that direction. In this case, however, there are some difficulties. In some regions of Africa, sickle cell anemia occurs with sufficient incidence to require a mutation rate of one in 100 for its maintenance, which Neel refers to with justification as "a truly staggering figure." The mutation rate for thalassemia is one in 2,500. The gene concerned in thalassemia is recessive, and Neel suggests that the disease can be maintained by a two per cent reproductive differential in favor of the heterozygotes as compared with the normal individual carrying no thalassemia gene at all. Obviously, in the case of sickle cell anemia, the reproductive differential must be greater. To support the mutation hypothesis a search has been made for infants exhibiting sickle cell anemia where both parents are normal. One such case has been found and is described.

The second group of papers on the "Genetic Analysis of Racial Traits" deals with the inheritance of normal characteristics, while the third group of papers is devoted to a specific facet of normal inheritance, i.e., that of blood groups. Lasker contributes a paper presenting in detailed fashion various characteristics of teeth which may be hereditary. He makes an interesting and impressive case in favor of the continued investigation of these structures, both because of their easy availability and because of the high rate of survival of teeth in human fossils.

Of the other papers in these two groups, Laughlin discusses the blood groups, morphology, and population size of the Eskimos. Spuhler deals with vein patterns, incidence of the peroneus tertius muscle, and the number of vallate papillae in the Navaho Indian. Race delivers himself of an excellent and eminently readable summary of the eight blood group systems and their inheritance, while Mourant discusses the incidence of the A, B, and O blood groups in the Mediterranean regions. The last paper of the group by Boyd, entitled, "Three General Types of Racial Characteristics," is the most general and perhaps the most interesting of the lot. He outlines the pitfalls involved in any interpretation of race on the basis of inherited characteristics in the same easy manner and daringly metaphoric style as is found in his book, "Genetics and the Races of Man." In rather gentle fashion, he expresses his doubts as to the value of distinguishing between human beings on the basis of cephalic index or more generally such systems as that of the "somatotyping" developed by Sheldon. He states—

"Certainly one may say that until a genetic mechanism which determines the various somatotypes in men and women has been worked out, the breakdown of human physique into graded amounts of just three components is no better founded scientifically than the old Greek analysis of all substances into four elements: air, water, earth, and fire."

The next group of talks on the subject of "Race Concept and Human Races" includes some of the most interesting papers in the symposia. Coon discusses the effect of cultural

characteristics upon genetic changes, particularly those cultural characteristics which affect the mating process. This would include not only the obvious customs of endogamy and exogamy but, for instance, decreases in fertility due to late marriages, contraception, abortion, celibacy, ritual mutilation, drugs, hot baths, and so on. He discusses in some detail the manner in which foreign genes can "leak" into a population isolate. Thus, there are the carnival times, the saturnalias, when ordinary sexual taboos are broken and forbidden matings, both exogamous, as between individuals from villages ordinarily without sexual contact, or endogamous, as in incest, may take place. Wife-lending and the privileged victim (i.e., a war captive who after a year of sexual freedom is executed) are also discussed. In one particular instance, Coon's analysis seems strangely incomplete. He states that since most fertile men can not produce fertile semen day after day, fertility is higher among those cultures where men are absent from their wives for days at a time. Cultures in which the male is frequently away hunting, or herding his cattle, or fishing, would therefore tend to have higher fertility than cultures involving a settled life. It strikes the reviewer as strange that Coon should assume that separation of husband and wife would automatically imply conservation of semen. There is always the possibility of masturbation, which in a proper analysis ought to have been mentioned even if only for the purpose of dismissing it.

Birdsell, in the longest paper in the symposia, delivers a detailed treatise interpreting genetic variations among Australian aborigines on the assumption that a given gene is introduced at one point of the continent and then drifts outward from that point. The gene-flow methodology, as he calls it, allows for an evaluation of the influence of various topographical and ecological barriers in impeding gene flow. The influence of such a technique in the wider world outside Australia could, with increasing knowledge, introduce a completely independent method for tracing the migrations of human groups, information concerning which is now misty due to lack of documentation.

In what is perhaps the most urbane paper presented at the symposium, Montagu presents his views on the concept of race. In it, he expresses a somewhat wistful wish that the word "race" be wiped out altogether and the phrase "ethnic group" be substituted for it. He admits that such a substitution serves no real purpose scientifically speaking, since the definitions of the two terms would be identical. However, he points out that the connotation of the word "race" among non-scientists has become so unfortunate that any discussion of race by scientists almost certainly leads to undesirable interpretations, whereas the phrase "ethnic group" would be more neutral from the standpoint of emotional context. In other respects, the atmosphere of his paper is much like that of Boyd's "Genetics and the Races of Man."

The section concludes with a paper by Lundeman on the anthropology of Scandinavia and one by Angell on population size and microevolution in Greece.

It is difficult to know what to say about the papers contained in the next section labeled "Constitution." It deals with aspects of Sheldon's well known theory of somatotyping, and indeed one of the papers is by Sheldon in which he extends his ecto-, endo-, mesomorphic classification to some 5,000 females presented in photographs. It was found that mesomorphy was much less common among females than among males. Sheldon also presents two terms, the morphophenotype and the morphogenotype. The former is the apparent somatotype as seen by direct examination of the body; while the latter is the name for the original hereditary and continuing genetic influence which can not change after conception has taken place. The morphophenotype is of course a combination of the morphogenotype and various environmental influences such as diet, injury, and so on.

Garn correlates certain biochemical facts with somatotype in another paper of the series. Thus, he finds that there is high serum cholesterol among endomorphs and low serum cholesterol among ectomorphs. Seltzer, in the remaining paper of the series entitled, "Constitutional Aspects of Juvenile Delinquency," ventures into a field, however, quite saturated with possible danger. He attempts here to correlate juvenile delinquency with somatotype by studying 500 male juvenile delinquents in a reform school as compared with 500 nondelinquent controls. While such correlations can be made and Seltzer finds, for instance, that the delinquents presented far more cases of mesomorphic dominance, i.e., superiority in bone and muscle develcpment, than did the controls, the value of such correlations seems to the reviewer to be most dubious and, indeed, harmful. There is no reason to think that the somatotype is in any way the independent variable upon which the dependent variable, juvenile delinquency, depends. Both may be the outgrowth of a still more fundamental third factor, or the connection may be a trivial one. It may be, for instance, that mesomorphs are no more subject to delinquent impulses than are ectomorphs or endomorphs, but being better developed muscularly are less often afraid to carry their thoughts into action. This, of course, does not mean that a mesomorph *ipso facto* is more evil than an ectomorph or an

endomorph, for there are other ways in which evil may be displayed than in outright violence. Indeed, this type of study carries us back to the well known "weak-chin," "shifty-eye," and "villainous-appearance" comic strip level of human characterization. It would be most dangerous to give the general public the idea that science in any way countenances a theory that personal and temperamental traits can be determined from physical appearance.

During the discussion at the conclusion of Seltzer's paper, Montagu asked the following question, which I shall quote in part—

"I should like to ask Doctor Seltzer whether he has considered the possibility that the differences in physique in the delinquents may not have been the result of the delinquent's behavioral habitus rather than of their constitution. Being a delinquent is associated with a great deal of stress and strain. It has recently been shown that emotional stress and trauma are frequently productive of nutritional disturbances which are capable of bringing about remarkable bodily changes. . . . I wonder what Doctor Seltzer's opinion would be in this connection."

To this is appended an editorial note as follows, "Doctor Seltzer did not wish to make any reply to this comment." Not having attended the conference, this reviewer is of course unable to judge accurately the subtle nuances involved in this exchange, but on the basis of cold print alone, it seems strange to the reviewer that such a significant question should meet with no response at all.

There is no doubt in the reviewer's mind but that if Doctor Seltzer were to take the trouble to attempt to correlate juvenile delinquency, or indeed any other personality trait, with the sign of the Zodiac presiding at the time of the individual's birth, he might find out a great many facts of interest in connection with the ancient science of astrology.

The symposium concludes with a section on "Perspectives of Future Research," including a paper by Dobzhansky on "Human Diversity and Adaptation," and one by Kluckhohn and Griffith on "Population Genetics and Social Anthropology." Dobzhansky's paper in particular is remarkable as a lucid and interesting presentation of the interrelationships of genetics and anthropology.

NOTES ON EVOLUTIONARY LITERATURE

ERNST MAYR

Advances in genetics.[1] The fourth volume of this review series contains nine contributions. Two deal with the genetics of important cultivated plants, coffee (Krug and Carvalho) and rice (Nagao), and one with the methods of cotton breeding. Two are devoted to physiological genetics, the action of certain genes on development in the mouse (Glücksohn-Waelsch), and of lethal genes on the development in *Drosophila* (Hadorn). There is much in both contributions of considerable interest for the gene-character problem. Hannah reviews the heterochromatin problem in *Drosophila melanogaster* and Stephens the question of possible significance of duplication in evolution. Matthey gives a short English resumé, as well as recent additions to his *Chromosomes des Vertebrés.*

The contribution in this volume that is perhaps of the greatest interest to the evolutionist is White's extensive review of cytogenetics among orthopteroid insects (pp. 267–330). It begins with a listing of the variation in chromosome number in the various taxonomic subdivisions of the orthoptera. In most groups the number and morphology of the chromosomes is rather constant. For instance, as far as known, all Grouse Locusts (Tetrigidae) have $2n = 13$ (♂), 14 (♀). However, in some groups, as in crickets of the genus *Nemobius* and certain walking sticks (*Isagoras*), there is much difference from species to species. The so-called chromosomal races of mole crickets (*Gryllotalpa*) are interpreted as sibling species. Nearly all orthopterans have the XO (♂), XX (♀) sex chromosome pattern. It can often be shown that possessors of deviating mechanisms form monophyletic groups. Perhaps the most interesting section of White's review is that on cytological polymorphism which includes some of the author's most recent researches. Different populations of the same species may differ in inversions, translocations, and supernumerary chromosomes. Just why some species have much of this polymorphism while it is reduced or absent in others is not clear, nor is the selective significance of much of the geographical variation in these phenomena as yet evident.

Population data on a species of tit-mouse.[2]

[1] Advances in genetics. Edited by M. Demerec, vol. IV, 343 pp., illustrated, $7.50, Academic Press, N. Y.

[2] Kluijver, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea, **39**: 1–135, 16 figs., 52 tables.

Even though everyone now emphasizes that the population is the basic unit of evolution and even though the various population parameters have been extensively studied theoretically by population mathematicians, it is appalling how little we actually know numerically of natural populations. Any study is welcome that helps to fill this gap, particularly if it is as thorough as Kluijver's work. Of special importance to the evolutionist are the following facts about a given local population: density (absolute size), reproductive success, immigration and emigration, mortality and longevity rates. Kluijver produces a wealth of data on all these points. His study of the Great Tit (*Parus major*) is based on data collected from 1912–1950, covering with particular thoroughness the last seventeen years. More than 10,000 broods were analyzed and more than 7,000 birds banded in the study area. The fact that the Great Tit readily accepts artificial nesting boxes for nesting and winter roosting greatly facilitated the study. The study area comprised 129 ha. The results were compared with several other areas where similar studies were made.

Pairs stay together for a second brood and remate the next year in about 80 per cent of the cases where both birds were surviving. The majority of locally born birds were found breeding 200–800 meters from their birth place, which corresponds to about the distance the family flock gets before it breaks up. Great Tits are territorial; the size of the territory is usually 2–3 ha., occasionally down to .5 ha., depending on the quality of the area.

In England all Great Tits are residents; in western Europe about 15 per cent, and in eastern Europe up to over 50 per cent are migratory. A high percentage of the migrants, but not all, are young birds. Some apparently settle 50–150 kilometers from their birth place, a few perhaps even farther.

About 33 per cent of the old and 21 per cent of the first year females make a second brood. There is an inverse correlation between population density and percentage of second broods. In very dense populations the percentage of second broods is less than 10 per cent but with densities of less than 4 pairs per 10 ha. it rises to 40–100 per cent. Comparisons of the same habitat in different years proves that this difference is not a matter of the habitat. This is evidently an important regulatory mechanism. Since clutch size also varies with density it is evident that fecundity in the Great Tit is conspicuously density-dependent. There seemed to be abundant food in the densely populated habitats, but also a greatly increased frequency of territorial disputes which consumed much of the bird's time and energy.

Disappearance of individuals is due either to death or emigration. The value of either factor can be determined only by indirect methods. In resident adults all loss is due to mortality, in first-year birds loss due to emigration is roughly balanced by gain through immigration. Mortality in first-year birds is 87 per cent as compared with an annual mortality of 49 per cent in older birds. Of the 456 birds which in 8 years bred for the first time in the study area, 162 (35 per cent) had been raised in the study area, the other 294 (65 per cent) were immigrants. This gives some indication of gene flow. The mortality rate of adults seems to be constant so that less than 1 per cent of the titmice reach an age of 8 years. A comparison of 5 localities through 12 years shows that fluctuations in population density are usually synchronous, although some rather large deviations seem to be due to purely local factors. At low population densities there is close correlation between population size and productivity of the previous year. At high populations densities high productivity may produce heavy emigration (apparently induced by overpopulation) and low population density during the next breeding season unless compensated by immigration. Similar correlations between high population density and emigration have been established by many authors for various species of vertebrates and invertebrates.

With the exception of the Brown Rat (*Rattus norvegicus*) this is the first study of a free-living animal proving the great importance of density dependent factors in productivity, population structure, and dispersal. It shows that the locally adapted genotype has unexpectedly great capacity of phenotypical variation. This plasticity results in a maximum utilization of the habitat; in years of low density a high number of young is produced, in years of high density high emigration takes place, leading to an occupation of previously underpopulated areas.

In a critical review of this study Lack [3] proposes the hypothesis that the available food supply is actually the basic factor which controls the various "density dependent factors" such as clutch size, number of second broods, and emigration. This raises a whole new set of questions. Kluijver's work is highly recommended for close study; it allows a remarkable insight into the fascinating field of population study.

Evolution in parasites.[4] Perhaps no other group of animals shows as much adaptive evo-

[3] Lack, D. 1952. Reproductive rate and population density in the Great Tit; Kluijver's study. Ibis, **94**: 167-173.

[4] Baer, Jean G. 1951. Ecology of animal parasites. Univ. Illinois Press, Urbana, 224 pp., 162 figs.

lution as the parasites. Unfortunately, much of the literature on the subject is exceedingly scattered and difficult of access to the non-specialist. We must be very grateful to Baer for a masterful account of the adaptations of animal parasites which might have been entitled with equally good reason: Evolution in Animal Parasites. All of us are familiar with the effects of parasitism on the intestinal tract (reduction often to the point of complete disappearance), egg number, sexuality, and attachment organs of the parasite. Here they are discussed for representatives of the 12 phyla from which parasitism has been reported. The question of host specificity is discussed, where not only the matter of speciation is involved, but also that of the origin (and sometimes secondary loss) of complicated life cycles involving multiple hosts. The phylogenetic facts are now emerging from such studies, but there still seems little known about the dynamic-evolutionary aspects: how are new hosts acquired and what selective advantage is there in a complicated life cycle? As the knowledge of parasites increases, an attack of these unsolved problems should be possible.

The Origin of an adaptive complex.[5] Goldschmidt reported some years ago on a fascinating adaptation in a fungus midge (Mycetophilidae) of New Zealand. The larvae build a sticky net at the roof of caves and attract to it midges and mosquitoes with the help of luminescence. This whole adaptive complex seemed so well integrated that it appeared difficult to Goldschmidt to visualize how it could have originated step by step through gradual evolution. Goldschmidt now reports from the literature additional cases in at least five genera, belonging to several subfamilies, in which carnivorous mycetophilids have developed some of the above adaptations without others. Some of these seem to have been independently acquired. The faculty to produce luminescence and to live in large colonies is limited to Araschnocampa of New Zealand.

Vector, disease, and evolution.[6] Several cases have become known in recent years where insect vectors of plant virus diseases feed preferentially and reproduce much faster on diseased plants than on healthy ones. There is an evident selective advantage for the virus to change the plant in such a way as to be beneficial to the vector. Presumably there is counter selection against the effects of the disease becoming too drastic. The plant, the virus, and the vector thus form a single evolutionary unit.

Evolution among fishes of Lake Tanganyika.[7] Rapid recent increases of our knowledge of the ecology and taxonomy of Tanganyika fishes and of the geology of the Tanganyika basin permit a reconstruction of the evolution of the remarkable fish fauna. Lake Tanganyika appears to have been formed in early Pliocene at the location of existing bodies of water (swamps?, ponds?) which drained to the Congo Basin. The early fish fauna was adapted to life on sandy and muddy shores and rocky beaches. As the lake deepened, pelagic and bottom forms evolved. Inequalities in the ecology of the shore line (rocky stretches separated by muddy estuaries, etc.) and rapid fluctuations of the water level provided the extrinsic factors permitting frequent speciation. The lake had a much lower water level during long periods dividing it into two separate, much smaller, but still very deep basins. Perhaps, as a result of this, it is found that almost half the species of *Haplochromis* are restricted either to the northern or southern portion of the Lake. More than half of the Lake Tanganyika fishes are cichlids, all of them endemic. Non-endemics occur among the other fish families, particularly among the old primitive fishes. Other Congo fishes have reached the Lake through the recently established Lukuga connection. Of the non-cichlids most occur along the shores and in the adjacent rivers. Of the cichlids only 4 species are restricted to adjacent rivers, 12 species occur in rivers and the lake, all others are restricted to the lake and belong (with one exception) to genera endemic in Lake Tanganyika. Entering the previously vacant pelagic and benthonic niches has thus led to considerable evolutionary acceleration. Poll presents detailed data on the ecology and the specializations of these genera.

Circular overlap.[8] The skylarks (*Alauda*) of the Old World consist of a northern, largely migratory group of subspecies (*arvensis*) which extends across all of Eurasia, and a southern, largely sedentary group (*gulgula*) of 11 subspecies, ranging from India to China and the Philippines. The two groups breed in the same districts from eastern Persia and northern Afghanistan through most of Russian Turkestan and must therefore be considered two separate species. However, on the Japanese islands (Kyushu, Hondo, Hokkaido) and on Sakhalin, a series of populations occurs

[5] Goldschmidt, R. B. 1951. Eine weitere Bemerkung über "Glühwürmer und Evolution." Naturwiss., **38**: 437–438.

[6] Kennedy, J. S. 1951. A biological approach to plant viruses. Nature, **168**: 890–894.

[7] Poll, M. 1950. Histoire du peuplement et origine des espèces de la faune ichthyologique du Lac Tanganika. Ann. Soc. R. Zool. Belg., **81**: 111–140.

[8] Vaurie, C. 1951. A study of Asiatic larks. Bull. Amer. Mus. Nat. Hist., **97**: 431–526.

which connects clinally the Chinese subspecies of *gulgula* with the east Siberian populations of *arvensis*. These populations could be equally well associated with either "species."

Speciation in bees.[9] All the known species (about 20) of the bee genus *Proteriades* have been found only in California and adjacent states. They are specialized to collect pollen from flowers of *Cryptantha* (records from 5 species so far). One species of bee may visit 2 or 3 species of *Cryptantha*. Speciation seems to be geographical since there are good subspecies, even within this limited range. Different subspecies of the same species may visit different species of *Cryptantha*, presumably correlated with differences in their distribution. Analyses like the present one help to explain changes in host specificity.

Olfactory isolating mechanisms.[10] This review of research on sexual scents in lepidoptera is most welcome in view of their great potential importance as isolating mechanisms. Many of the scents are not species specific but also stimulate the males of closely related species. Additional isolating mechanisms prevent hybridization.

Subspecies in paleontology.[11] A further plea to distinguish clearly between subspecies based on populations, and varieties based on individuals. Discusses several cases where the use of subspecies clarifies a problem of variation or evolution. Suggests to distinguish between "phylogeny" being the history and "phylogenesis" being the process of evolution.

The genetics of characters.[12] Our basic knowledge of genetics is derived from an analysis of the units of inheritance, genes and mutations. Though admitting the fundamental value of this type of research, the evolutionist has always felt a little frustrated by it because it did not seem to shed too much light on the evolution of phenotypes which are the product of intricate gene complexes. In this, the evolutionist found a sympathetic ally in the practical animal breeder, who always has the best results by forgetting all about individual genes and concentrating on the improvement of the overall genetic basis of the desirable phenotype (e.g., high milk production in dairy cattle, high egg number in poultry). That this genetic technique has ultimately the same scientific basis as the analysis of single Mendelian characters is sometimes ignored, as is evident from the arguments of some of older paleontologists and the Lysenkoists. Such arguments are based on an ignorance of polygenic genetics. As Mather and other geneticists have emphasized, observed characters have only rarely a simple genetic basis, and new types of analysis are needed to shed light on the genetics of polygenic characters. Lerner's work is the best treatise known to me dealing with this field. Even though the data on which it is based are derived almost entirely from egg production in chickens and are spiced with a certain amount of mathematics, the volume should be read by every evolutionist. It will help him to understand better the interaction of genetic factors in the production of characters (the phenotype), the respective roles of environmental and genetic factors, the effects and limits of selection, and other aspects of genetics that are of vital importance to the evolutionist. It is important to realize, as the author states, that up to now only the surface has been scratched in this field.

Peripherally isolated populations.[13] Aberrant populations are found along the western periphery (Orkneys, Channel Islands, etc.) of the range of 5 European species of voles. These are interpreted by Zimmermann as relic populations of forms that had a wider distribution during the Pleistocene but have since been eliminated in most mainland areas by other more successful subspecies. The selective situation does not seem to have been sufficiently considered in this and similar studies. If in a warm period a large-sized population on the mainland is replaced by a small-sized one, this does not necessarily prove a changing of population by migration. The change in size could as well be due to a genetic alteration of the mainland population as a consequence of selection pressure. The large-sized island population might be explained as adaptive. Much that is known about morphological changes in recently isolated mammal populations contradicts the notion that size is a conservative character. The fact that neighboring islands are frequently occupied by populations with very different phenotype also indicates rapidity of morphological change.

Puzzling polymorphism.[14] The mosquitoes of the *Anopheles maculipennis* group continue

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[9] Timberlake, P. H., and C. D. Michener. 1950. The bees of the genus *Proteriades*. Univ. Kansas Sci. Bull., **33**: 387–440.

[10] Götz, B. 1951. Die Sexualduftstoffe an Lepidopteren. Experientia, **7**: 406–418.

[11] Sylvester-Bradley, P. C. 1951. The subspecies in paleontology. Geol. Magazine, **88**: 88–102.

[12] Lerner, I. M. 1950. Population genetics and animal improvement. As illustrated by the inheritance of egg production. Cambridge Univ. Press, 342 pp.

[13] Zimmermann, K. 1950. Die Randformen der mitteleuropäischen Wühlmäuse. Syllegomena Biologica, 454–471.

[14] Frizzi, G. 1951. Dimorfismo chromosomico in *Anopheles maculipennis messeae*. Scientia Genetica, **4**: 79–93.

to be puzzling. The work of previous authors, as summarized by Bates, seemed to indicate the presence of 6 sibling species, camouflaged as "varieties" in most of the literature. Frizzi's studies reveal new complications. Each of the species *A. labranchiae, atroparvus, sacharovi,* and *maculipennis* is distinguished by a specific gene arrangement in the salivary chromosomes but no geographic variation has so far been found in any of the four species nor any intrapopulation polymorphism. Only *A. messeae* has two gene arrangements; one consists of a homozygous inversion in the right arm of the third chromosome, equal to that in *maculipennis;* the other has, in addition, a profound rearrangement (with at least 5 breaks) in the X-chromosome. Is this a case of balanced polymorphism or are we dealing with two exceedingly similar sibling species? Frizzi's investigations have not proved either assumption. The eggs of this population are very variable ranging from largely gray (considered characteristic of *messeae*) to completely black (considered typical of *melanoon*); the floats are striated. There is no correlation between the variation in the gene arrangements and that in the egg coloration. In a transect through the Po valley the standard gene arrangement had its highest frequencies at higher elevations and in the cooler part of the year; the inverted arrangement at hot and humid locations and during the hottest parts of the year. These data are consistent with balanced polymorphism, except that among many hundred captured mosquitoes only 1.6 per cent were inversion heterozygotes instead of 40.6 per cent as should be expected on the basis of the frequency of the two gene arrangements. The gonads of the heterozygotes are completely normal, thus they cannot be species hybrids. The low frequency of the heterozygotes is ascribed to nonrandom mating, but there is as yet no experimental proof for this assumption.

Polymorphism and sex in isopods.[15] In the terrestrial isopod *Porcellio scaber* a mottling gene occurs with a frequency of ± 25 per cent in European populations. This gene, an autosomal dominant, affects the sex ratio. Recessive homozygous strains have a surplus of males (usually 65–75 per cent ♂), strains with the color gene (homozygous or heterozygous) have a large surplus of females. Apparently homologous genes with the same effects are found also in other genera. The selective significance of this obvious case of balanced polymorphism has not yet been analyzed. There was no conspicuous mortality differential among juveniles.

Polymorphism in a marine isopod.[16] In the marine isopod *Sphaeroma serratum* of the French Channel coast, considerable color polymorphism is primarily due to one locus with at least 5 alleles. One is a universal recessive and the others form an ascending epistatic series in which each member is dominant to the inferior alleles. Thus the genetics of this polychromatism corresponds to that in many other animals (grasshoppers, coccinellids, etc.). Additional genes are either further members of the same allelic series or independent genes. There is only one brood per year and difficulties of maintenance in the laboratory do not make these isopods ideal genetic material.

Each natural population on the coasts of France has a characteristic frequency of these genes, but throughout several years no seasonal or other temporal changes in gene frequency could be ascertained in most populations with the statistical techniques employed by the authors. On the whole, the more dominant a gene in the epistatic series, the rarer it is in the population. In an isolated population at Morgat there is seasonal variation in the frequency of the spotting gene *discretum,* which is dominant only to the universal recessive *albicans.* In June of two years among 4533 individuals 23.39 ± .48 per cent had the gene and in September among 2085 individuals 28.03 ± .77 per cent. The difference of 4.64 ± .90 per cent is highly significant. Geographical trends are apparent in the frequency of some of the alleles along parts of the coast; others appear to vary quite irregularly. The rare alleles appear to be absent at certain stations. No correlation has yet been established between these gene frequencies and local environmental factors.

Modification of the phenotype.[17] Two species of *Coregonus* from the same North Swedish lake, which agree in growth rate and body proportions but differ in number of scales and gill rakers, spawning season, and choice of spawning ground, were transplanted separately into two vacant lakes. The species placed in a lake with superior food supply showed accelerated growth, the other in a poor lake retarded growth. Both differed greatly in their body proportions. The difference in scale numbers disappeared in fingerlings raised under identi-

[15] de Lattin, G. 1951. Untersuchungen über die geschlechtsbeeinflussende Wirkung von Farbfaktoren bei Porcellio und Tracheoniscus. Z. Vererbungslehre, **84**: 1–37.

[16] Bocquet, C., C. Lévi, and G. Teissier. 1951. Recherches sur le polychromatisme de *Sphaeroma serratum* (F). Arch. Zool. Exper. Gén., **87**: 245–297, col. pl.

[17] Svärdson, G. 1950. The Coregonid problem II. Morphology of two Coregonid species in different environments. Inst. Fresh-Water Research, Drottningholm, Report No. 31: 151–162.

cal conditions. Neither of these two characters is thus decisive in classifying populations of *Coregonus*. The difference in the number of gill rakers—though narrowed somewhat—remained after transplantation and seems to have the strongest genetic component among the phenotypic characters used in *Coregonus* taxonomy.

No rapid change of phenotype.[18] In Lake Laach in western Germany some *Coregonus* were introduced in 1871 which have been quoted since 1912 as a particularly striking case either of rapid evolutionary change or of phenotypic plasticity. These fish were reported to have been a well-known "variety" from the Lake of Constance and to have changed their characters drastically in the 40 years since their release. Wagler now presents weighty evidence indicating that actually a very different race (from one of the Swiss lakes) had been introduced and that there is no evidence for any major change of type. The Lake of Constance race, introduced experimentally in 1939, had not changed significantly by 1950.

Climate and body proportions.[19] A study of the geographic variation in 11 species of amphibians and 26 species of reptiles shows a few regularities. Drought tolerant amphibians are largest, humidity-dependent species smallest in the warmest parts of their range; the latter have longer extremities in the warmer parts of their range. Among the lizards long tails are found in island populations, the longest legs where the maximum substrate temperatures are highest.

Geographic variation in competition tolerance.[20] The two species of salamanders *Plethodon glutinosus* (low altitudes) and *P. jordani* (high altitudes), are altitudinal representatives over most of their ranges; the maximum observed overlap being 200 feet. Two subspecies of *jordani*, however, descend much lower and nearly their entire altitudinal range is overlapped by *glutinosus*. The two species thus avoid competition over the greater part of their ranges, but co-exist in others, apparently due to geographical variation of tolerance in *jordani*.

Physiological races in oysters.[21] Much recent research has shown that geographical races of the oyster differ in temperature tolerance. Most oysters from southern New Jersey and Virginia failed to spawn when kept in Connecticut waters. Gonadal material was resorbed at the end of the breeding season. Northern oysters, taken into warm southern waters, discharge their gametes long before the local population. Such adaptation to local water conditions, particularly temperature, seems to be widespread in marine animals.

The filling of vacant niches.[22] One would think that the Mediterranean with its rich fish fauna would have no room for further arrivals. Nevertheless, 15 species of fish have colonized the area, coming from the Red Sea since the Suez Canal was opened in 1869. Some of these must have moved with an average rate of 300 meters per day! No Mediterranean fish has succeeded in entering the Red Sea. There is much to indicate that it is the greater ecological tolerance of the Red Sea fishes which favored their spread. Some of them had already existed in the Mediterranean in pre-Pleistocene times, and it is somewhat of a puzzle why they had ever become extinct, in view of their great temperature and salinity tolerance.

Host plants and polymorphism.[23] The various genetic types within polymorphic populations of the lady beetle *Harmonia axyridis* in southern Japan show different frequencies on different host plants. For instance, *conspicua* occurred with a frequency of 12 per cent (1950)—31 per cent (1949) on pine as against 40 per cent (1949)—62 per cent (1950) on wheat, *axyridis* with a frequency of 20 per cent (1949)—33 per cent (1950) on pine as against 7 per cent (1949)—11 per cent (1948) on wheat. The recessive gene for the absence of an elytral ridge occurs in 97 per cent of the population on pine trees as against 80 per cent of the population on wheat. The frequency of the various genes on wheat agrees fairly closely with that of fruit and other deciduous trees locally and in adjacent districts. There are no dispersal barriers between the pine trees and the other plants. The differences are evidently due to differential mortality or to differential habitat

[18] Wagler, E. 1951. Die Felchen (Coregonen) des Laacher Sees. Zool. Anz., **147**: 180–187.

[19] Schuster, O. 1950. Die klimaparallele Ausbildung der Körperproportionen bei Poikilothermen. Abh. Senckenb. Naturf. Ges., no. 482, 89 pp., 2 plates.

[20] Hairston, N. G. 1951. Interspecies competition and its probable influence upon the vertical distribution of Appalachian salamanders of the genus *Plethodon*. Ecology, **32**: 266–274.

[21] Loosanoff, V. L., and C. A. Nomejko. 1951. Existence of physiologically different races of oysters, *Crassostrea virginica*. Biol. Bull., **101**: 151–156.

[22] Kosswig, C. 1950. Erythräische Fische im Mittelmeer und an der Grenze der Ägäis. Syllegomena Biol., 203–212.

[23] Komai, T., and Y. Hosino. 1951. Contributions to the evolutionary genetics of the lady beetle *Harmonia*. II. Microgeographic variations. Genetics, **36**: 382–390.

selection of the different genotypes or both. No data are presented that permit choice between these causes.

Fluctuations in species borders.[24] About 20 per cent of the central European birds have shown notable fluctuations of their species border during recent decades. Twelve to 14 species have disappeared, at least 15 species have invaded the area or, at least, greatly expanded their range. Some of the immigrants come from the east (Asia via Russia), others from the south and southeast. Man-made changes of the landscape are in part responsible, but climatic changes are responsible for most range changes, as convincingly demonstrated by Kalela.

What is "the same habitat"? [25] Elton in a recent analysis of the number of species per genus in a given habitat interpreted his figures as confirmation of Gause's rule that two closely related species cannot co-exist in the same habitat. Williams re-analyzing the same data by a different statistical method came to the seemingly opposite conclusion, namely, that in a given habitat more species per genus were found than in a random sample of the respective fauna. Bagenal shows that Williams' observation is correct so far as heterogeneous habitats are concerned [26] but that in a homogeneous habitat, a true "niche," Gause's rule is valid. Obviously in such heterogeneous habitats as marshes one will get several species of rails and herons, and in forest treetops many species of warblers and flycatchers, but within these habitats each species occupies its own particular niche.

[24] Niethammer, G. 1951. Arealveränderungen und Bestandsschwankungen mitteleuropäischer Vögel. Bonner Zool. Beitr., **2**: 17–54.

[25] Bagenal, T. B. 1951. A note on the papers of Elton and Williams on the generic relations of species in small ecological communities. Jour. Anim. Ecol., **20**: 242–245.

[26] See also Williams, C. B. 1951. Intrageneric competition as illustrated by Moreau's records of East African bird communities Jour. Anim. Ecol., **20**: 246–253.

SOCIETY FOR THE STUDY OF EVOLUTION

Sixth Annual Meeting, Berkeley

Report of the Secretary for 1951

Minutes of the Council Meeting: held on June 25, 1951 at 5:45 p.m. in the Men's Faculty Club, University of California, Berkeley 4, California.

In Attendance:

Vice-Presidents: Jens C. Clausen and E. B. Ford.
Secretary: Theodor Just.
Council Members: G. L. Stebbins, Jr., R. A. Stirton and C. L. Hubbs.

President Theodosius Dobzhansky was prevented from attending by an automobile accident and Treasurer K. P. Schmidt by a strike of airplane personnel.

The group asked Vice-President E. B. Ford to deliver the public address scheduled for June 27th. Prof. Ford graciously accepted this invitation.

The group authorized the payment of $15.00 to Dr. G. L. Stebbins to cover the cost of printing the posters for this public lecture. Dr. Stebbins was paid out of funds accumulated by the Local Committee.

The group considered the invitation to meet with the A.A.A.S. in San Francisco in 1954, should such a meeting materialize. In regard to future meetings the following policy was adopted: the Society should meet one year with the AIBS, another year with the Geological Society of America, another year with the A.A.A.S., and a fourth year by itself. This policy of rotating its meetings will give the Society the greatest freedom of operation and the most diversified contacts for its purpose. Suitable symposia arranged for other meetings but within the scope of the Society may be cosponsored by the Society for the Study of Evolution, although its annual meeting may be held at a different time and in a different place. It was decided that in 1952 the Society should meet with the A.I.B.S. in Ithaca, New York, September 8–10.

The group discussed the possibility of printing the membership list in an issue of the journal, to be followed at suitable intervals by supplementary lists, as the cost of the separate printed list was too high and the available funds can be used to better advantage by enlarging the journal.

An application for a complimentary set of Evolution received from the Science Museum, South Kensington, London was rejected. The following policy was adopted: the Nominating Committee for 1952 should prepare a list of particularly outstanding men in foreign countries to whom Evolution should be sent free. The total number of complimentary sets should be limited. Dr. Stebbins recommended Professor Hitoshi Kihara, Kihara Institute, University of Kyoto, Kyoto, Japan as a candidate.

The proposal by former Vice-President Lee Dice made at the Columbus meeting concerning retiring presidents becoming automatically members of the Council could not be acted on as only six members of the Council were present.

The group expressed its thanks for the efficient work of the Local Committee to its Chairman, Dr. G. L. Stebbins.

As the meeting was held so early in the year, neither the Editor nor the Treasurer were able to present complete reports concerning their activities. Mr. K. P. Schmidt who wanted to retire at the time of the meeting was unable to do so as the new Treasurer did not return to New York until September 1, 1950.

Business Meeting: June 26, 1951.

The Business Meeting was held before the morning session on June 26th. The Secretary read the results of the elections as follows:

President: E. B. Babcock, University of California.
1st Vice-President: K. P. Schmidt, Chicago Natural History Museum.
2nd Vice-President: H. J. Muller, Indiana University.
3rd Vice-President: Åke Gustafsson, Sweden.
Treasurer: C. M. Bogert, American Museum of Natural History.
Councilman: S. Wright, University of Chicago.
Councilman: A. H. Miller, University of California.

The Secretary also announced that Vice-President E. B. Ford had agreed to deliver the public address on "Creative Evolution" in place of President Dobzhansky who was prevented from coming by an automobile accident.

The Secretary informed the membership that the next meeting would be held under the sponsorship of A.I.B.S. at Cornell University, Ithaca, New York, September 8–10, 1952.

The Secretary asked the membership to authorize the Chairman of the Local Committee to send a telegram to President Dobzhansky then at Mather, California wishing him a quick recovery.

The Secretary asked the membership to extend an official vote of thanks to the Local Committee for its efforts in making the meeting the success it was.

All announcements and recommendations of the Council were approved in toto.

The dinner meeting held in the evening of June 26 was attended by 84 persons. A total of 125 persons registered for the meetings.

The public address on "Creative Evolution," scheduled for 8 p.m., June 27th, Auditorium, Life Sciences Building, Berkeley, was given by Vice-President E. B. Ford. The speaker was introduced by President-elect E. B. Babcock.

The public address on "Creative Evolution," scheduled for 8 p.m., June 27th, Auditorium, Life Sciences Building, Berkeley, was given by Vice-President E. B. Ford. The speaker was introduced by President-elect E. B. Babcock.

Respectfully submitted,

THEODOR JUST, *Secretary*